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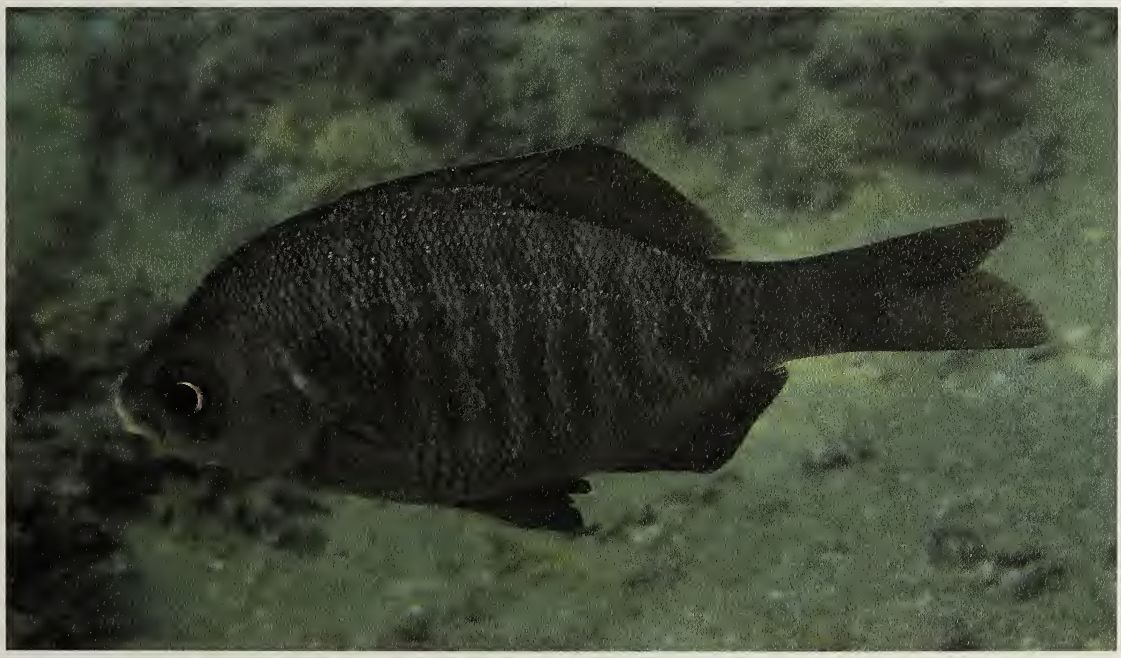

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Geometric Morphometric Differentiation of Two Western USA Lizards (Phrynosomatidae: Squamata): *Uta stansburiana* and *Urosaurus ornatus*, with Implications for Fossil Identification

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Abstract.—Squamate fossil identification has been challenging due to the incomplete understanding and sometimes complete lack of osteological research of extant species. Here we compared the maxilla of two similar species of phrynosomatids: *Uta stansburiana* (Common Side-blotched Lizard) and *Urosaurus ornatus* (Ornate Tree Lizard). Through landmark-based geometric morphometric analyses, we determined which characters significantly separated the two species. A principle component analysis (PCA) and a stepwise discriminant function analysis (DFA) were conducted, in which we compared 15 landmarks between *U. stansburiana* and *U. ornatus*. Both the PCA and stepwise DFA showed separation between the two species. The stepwise DFA selected five of the 15 characters as statistically significant, three of which are considered apomorphies and show promise for fossil identification. The first character is in the ventral region of the posterior maxilla process; *U. ornatus* has a defined notch, whereas *U. stansburiana* does not. The second and third characters are in the anterior portion of the maxilla, which is curved dorsally in *U. stansburiana*, whereas *U. ornatus* shows no curving. The results of this study are used to identify fossil *Uta* vs *Urosaurus*, but more analyses need to be conducted on other phrynosomatid species for comprehensive identification.

Identification of fossil squamate reptiles (lizards and snakes) is typically a challenge due to the lack of comprehensive osteological collections of extant taxa. As a result, identification of isolated cranial elements is usually based on modern distributions of extant taxa, which leads to circular reasoning (Bell et al. 2009; Bell and Mead 2014). Additionally, the osteological apomorphies and patterns of variation at the species and genus level are unknown in most living taxa, making accurate identification often questionable. What is known is aptly presented, for example, in Lundelius (1957), Conrad (2008), Bhullar (2011), and Gauthier et al. (2012). Without proper identification of these organisms, more complex questions involving extinction, speciation, and geographic distribution cannot be adequately addressed.

Here we analyze the maxilla of two closely-related species of the Phrynosomatidae from western North America: *Uta stansburiana* (Common Side-blotched Lizard) and *Urosaurus ornatus* (Ornate Tree Lizard). These two species are typically considered indistinguishable from one another based on jaw (dentary and maxilla) and dental characteristics (Norell 1989). This is a problem because the majority of Neogene-age squamate fossils identified tend to be dentary and maxillary bones often due to collecting biases (Bell and Mead 2014). In the study here, we use geometric morphometric analyses on one bone, the maxilla, to find statistically significant characteristics that can be used to distinguish *U. stansburiana* from *U. ornatus*.

Uta stansburiana is one of the most abundant lizards found today in arid and semi-arid regions of western North America (Stebbins 2003). Living *U. stansburiana* are easily identified by the presence of a dark blotch on their side near the forelimb. They are predominately terrestrial and are found around rocks and low-ground bushes. The present range for *U. stansburiana* is from central Washington to the tip of Baja California, north Sinaloa and north Zacatecas Mexico, along the Pacific coast to west Colorado and west Texas, and many islands off of Baja and southern California. Fossil *U. stansburiana* are known from a variety of locations across Arizona: Brass Cap Point, Desert Almond, Vulture Cave, and Welton Hills (Mead 2005). They are considered a common species in the region during the Holocene and Late Pleistocene (Rancholabrean Land Mammal Age). Holocene-age fossils are also known from Howell's Ridge Cave in southern New Mexico (Van Devender and Worthington 1977; Harris 1993).

Urosaurus ornatus is a climbing lizard and is typically found on rocks and trees (Stebbins 2003). Their habitat ranges from the desert to the lower edge of spruce/fir zones. Living *U. ornatus* are distinguished by the large scales on their back, which are interrupted along the mid-line by small scales. The present range of *U. ornatus* is from southwestern Wyoming to Nayarit and northern Coahuila, Mexico (including Tiburón Island in the Gulf of California), along the lower Colorado River valley central Texas, and into California to the Chuckwalla Mountains. Fossil *U. ornatus* are known from two locations in Arizona: Deadman Cave and Picacho Peak (Mead et al. 1984; Van Devender et al. 1991). Although *U. ornatus* is common in the region today, their fossil record is inadequately understood. Fossil forms are also known from Howell's Ridge Cave and U-bar Cave in southern New Mexico (Van Devender and Worthington 1977; Harris 1993).

Through geometric morphometrics, we determine if there is a morphological difference in the maxilla bone of *U. stansburiana* and *U. ornatus*. We predict there will be clear separation between the two groups. Also, we hope to obtain a list of statistically significant characters, which can be used to identify fossil forms using the maxilla. We picked these two taxa because our sample size of their skeletons was robust enough to be statistically sufficient. Correct identification of the isolated fossil skeletal elements is a problem for several species of phrynosomatids (Norell 1989; Bell et al. 2009), thus, we hope that this study will be the first step towards comprehensive fossil identification.

Materials and Methods

All modern specimens were in the ETSU (East Tennessee State University) vertebrate-paleo collections at the time of this study. Only disarticulated specimens were used to ensure consistent orientation. To reduce skewed results, only adults were used. To determine ontogenetic age, we checked the snout-vent length (SVL) data provided on the information tag of each specimen. According to Stebbins (2003), an adult *U. ornatus* SVL is 38-57 mm, and an adult *U. stansburiana* SVL is 38-63 mm. *Urosaurus ornatus* specimens were collected from: Arizona (counties: Pima, Coconino, Yavapai, and Cochise), Colorado, and Canyonlands National Park, Utah. *Uta stansburiana* specimens were collected from: Arizona (counties: Yavapai and Yuma), Yucca exit off of I-40 in Arizona, Burnt Springs Canyon at mile 259.5 along the Colorado River, Hidden Cave in Falon Nevada, San Bernardino county California, and a few unknown locations in California.

The bone selected for this study was the maxilla because they are common in the fossil record. Each specimen was photographed in labial view using a camera microscope. In labial view, the maxilla connects to the: jugal, lacrimal, pre-frontal, nasal, and pre-maxilla (Fig. 1A). The articulation surfaces with these bones have distinct processes, which are perfect for landmark locations (Fig. 1B). We selected the right maxilla, but if the right maxilla was unavailable or damaged, we used the left and reversed the image. Specimen orientation was consistent; the

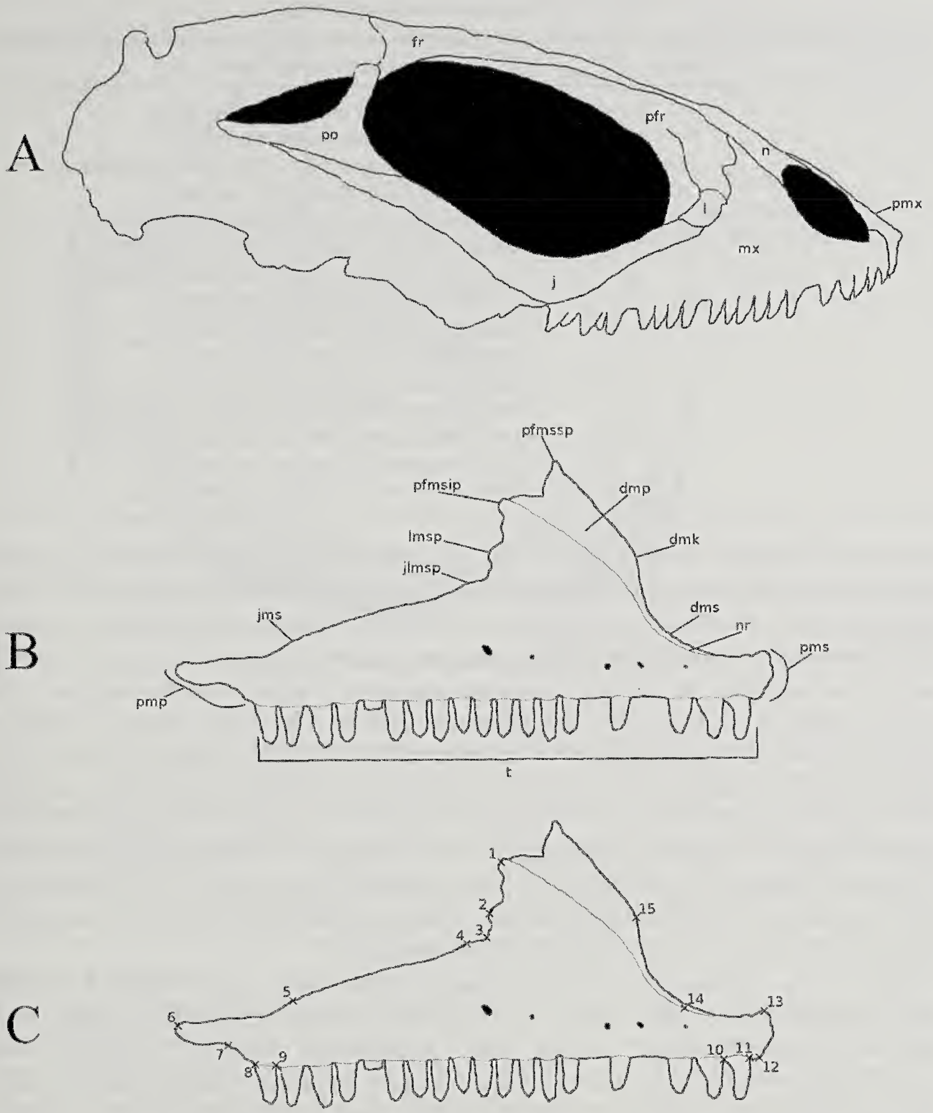

Fig. 1. A) Line drawing of *Urosaurus ornatus* skull showing the mx contact with: pmx, n, pfr, l, and j. B) Labeled diagram of *U. ornatus* maxilla in labial view. C) Location of landmarks on *U. ornatus* maxilla. See Methods and Materials for abbreviations.

premaxilla/maxilla suture, prefrontal/maxilla suture superior-process, and the palatine/maxilla suture (on lingual side) laid on an even piece of clay. Microscope photos were taken consistently at the same magnification. All photos were appended into a single thin-plate-spline (tps) file using tpsUtil (Rohlf 2016c). Next, a set of 15 2-dimensional landmarks were digitized onto 25 specimens of *U. stansburiana* and 24 specimens of *U. ornatus* using tpsDIG2 (Fig. 1C; Table 1; Rohlf 2016d). Landmark locations were predominantly on the perimeter of the maxilla and had to be present on every specimen in the analysis.

To align the data, we ran a single Procrustes fit using tpsSuper (Rohl 2016b). We used SPSS (IBM Corporation) to run the Principle Component Analysis (PCA) and the stepwise

Table 1. Description of landmark location.

Landmark	Location description
1	Tip of pfmsip: point of maximum curvature
2	Tip of lmsp: point of maximum curvature
3	Posterior base of dmp: point of maximum curvature
4	Tip of jlmsp: point of maximum curvature
5	Posterior ridge of jms: point of maximum curvature
6	Posterior tip of pmp: point of maximum curvature
7	Ventral notch of pmp: point of maximum curvature
8	Posterior base of the posterior most tooth
9	Anterior base of the posterior most tooth
10	Posterior base of the anterior most tooth
11	Anterior base of the anterior most tooth
12	Ventral edge of pms: point of maximum curvature
13	Dorsal edge of pms: point of maximum curvature
14	Curve of nr: point of maximum curvature
15	Tip of dmk: point of maximum curvature

Discriminant Function Analysis (DFA). The PCA was conducted to see if there is any initial separation between *Uta stansburiana* and *Urosaurus ornatus*. In addition, a stepwise DFA, with a significance level of 0.05, was also conducted on the data to examine separation and to determine which characters are significantly different between *U. stansburiana* and *U. ornatus*. Since this analysis was stepwise, the selected significant characters also showed little variation within a species which is important for determining apomorphies. Characters selected as significant by the stepwise DFA were examined in each specimen to determine consistency across both species. The PCA loading scores for each significant character on the first three components were reported to determine their contribution to the variance. Lastly, to test the mean differences in maxilla shape, a thin-plate-spline analysis was conducted to visualize species differences. To obtain a consensus for each species, we used tpsSuper (Rohl 2016b) to run a Procrustes fit for *U. ornatus* and *U. stansburiana* separately. Using tpsSpline (Rohl 2016a), we morphed the consensus of *U. ornatus* to the consensus of *U. stansburiana*.

Abbreviations. Abbreviations follow Hocknull (2000). **dmk**: dorsal maxilla kink, **dmp**: dorsal maxilla process, **dms**: dorsal maxilla process slope, **fr**: frontal, **j**: jugal, **jlmsp**: jugal/lacrimal/maxilla suture process, **jms**: jugal/maxilla suture, **l**: lacrimal, **lmsp**: lacrimal/maxilla suture process, **mx**: maxilla, **n**: nasal, **nr**: naris ridge, **pfmsip**: prefrontal/maxilla suture inferior-process, **pfmssp**: prefrontal/maxilla suture superior-process, **pfr**: prefrontal, **pmp**: posterior maxilla process, **pms**: premaxilla/maxilla suture, **pmx**: premaxilla, **po**: postorbital, **t**: teeth.

Results

The PCA results are displayed in a 3-dimensional scatter plot where component score 1 is the X axis, component score 2 is the Y axis, and component score 3 is the Z axis (Fig. 2). The graph shows separation along the X axis (component 1) and along the Z axis (component 3). Separation is not clear along the Y axis (component 2); however, *U. stansburiana* data points have a wider distribution along the Y axis. Component 1 explains 24.47% of the variance with an eigen value of 7.34, component 2 explains 16.32% of the variance with an eigen value of 4.9, and component 3 explains 13.14% of the variance with an eigen value of 3.94.

Results from the stepwise DFA are displayed in a 2-dimensional bar-graph where the discriminant score 1 is on the X axis and frequency is on the Y-axis (Fig. 3). The graph shows

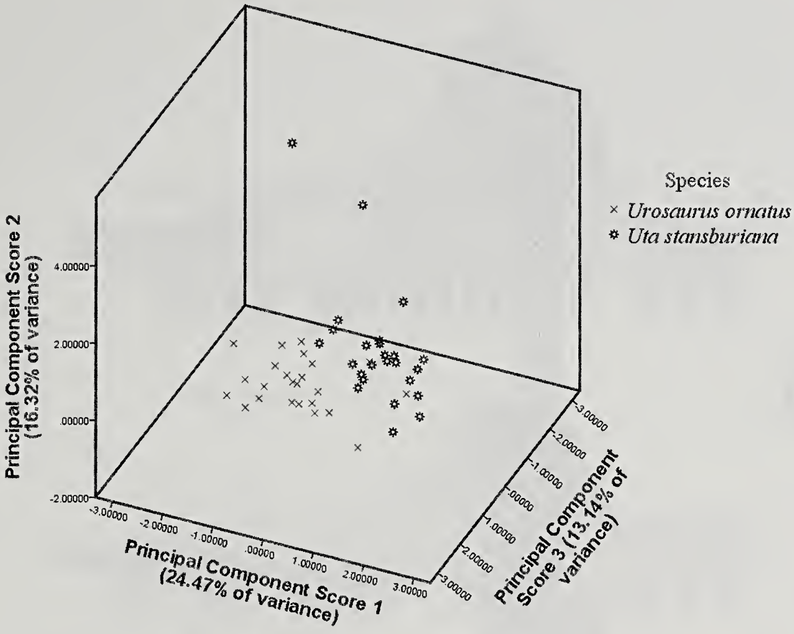

Fig. 2. Principle Component Analysis scatter plot.

clear separation (Fig. 3), with a significance value of 8.28E-19. The stepwise DFA selected five variables as statistically significant (Table 2). The PCA component loading scores and Wilk's Lambda values for each significant variable are listed in Table 2. Variables that consistently vary between *U. stansburiana* and *U. ornatus* are the ventral edge of the premaxilla/maxilla suture height (landmark 12, Y axis), posterior base of the anterior most tooth height (landmark 10, Y axis), ventral notch on the posterior maxilla process height (landmark 7, Y axis), posterior maxilla process tip height (landmark 6, Y axis), and lacrimal/maxilla suture process tip height (landmark 2, Y axis).

Component 1 has a high loading score for three of the significant variables: the ventral edge of the premaxilla/maxilla suture height, posterior base of the anterior most tooth height, and posterior maxilla process tip height. Component 3 loading score is high for the ventral notch on the posterior maxilla process height. The lacrimal/maxilla suture process tip height is the only significant variable to have a low loading score for all three components. Also, component 2 has a low loading score for all five significant characters.

Discussion

Both the PCA and the stepwise DFA show definitive separation (Fig. 2 and Fig. 3), which validates *U. ornatus* and *U. stansburiana* as morphologically separate species. PCA separation is observed along the X axis (component 1) and the Z axis (component 3). Of the five significant characters selected by the stepwise DFA, three have high loading scores on component 1 while one has a high loading score on component 3. Even though component 2 explains more of the variance then component 3, none of the significant characters had a high loading score on component 2. Additionally, separation is not clear along the Y axis (component 2) of the PCA; however, *Uta stansburiana* data points show more variation along the Y axis. This wide range amongst the *U. stansburiana* could be due to the species having more morphological variation

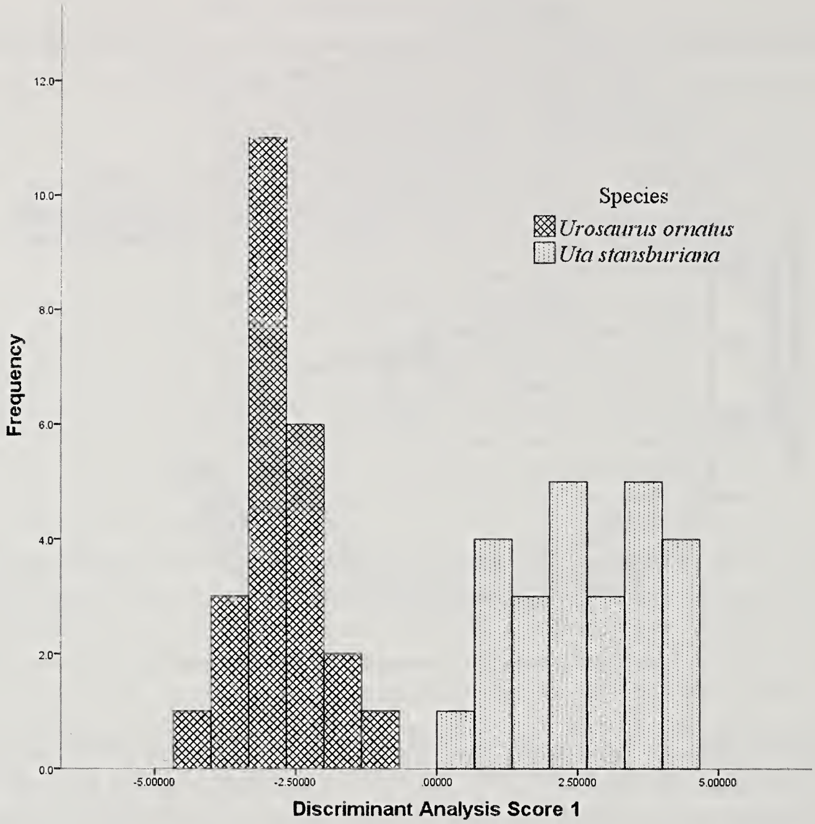

Fig. 3. Stepwise Discriminate function analysis bar graph.

compared to *U. ornatus*. Alternatively, the wide range could be due to abnormal specimens that are morphologically different from the rest due to pathologies, misidentification, or ontogenetic age. With a larger sample size collected from a variety of localities, the natural range of variation for each species would become clearer.

Based on the significant character's Wilk's Lambda values and observation of each specimen, the best three characters for differentiating *U. ornatus* from *U. stansburiana* are: 1) the ventral edge of the premaxilla/maxilla suture height, 2) the posterior base of the anterior most tooth height, and 3) the ventral notch on the posterior maxilla process height. These three statistically

Table 2. Variables kept by stepwise Discriminant function analysis.

Variables kept by stepwise DFA	Wilks' Lambda value	Significance score	Loading score from PCA for component 1	Loading score from PCA for component 2	Loading score from PCA for component 3
Y12	0.449	1.66E-10	0.841	−0.160	−0.359
Y10	0.219	2.71E-16	0.747	−0.478	0.230
Y7	0.133	5.41E-18	0.421	0.197	0.723
Y6	0.158	1.26E-18	0.693	0.248	−0.335
Y2	0.134	1.10E-18	−0.550	−0.262	−0.386

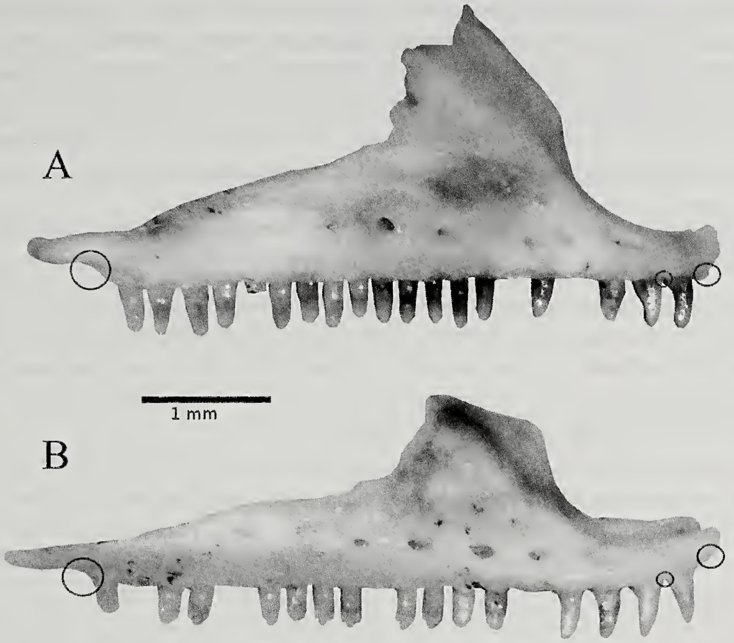

Fig. 4. Right maxilla in labial view: A) *Urosaurus ornatus* example specimen (JIM 0137) and B) *Uta stansburiana* example specimen (FB 1678). Statistically significant characters that were consistently observed in all specimens are circled.

significant characters had the highest Wilk's Lambda values (Table 2), and when examining each specimen of *U. ornatus* and *U. stansburiana*, these differences are very apparent. Fig. 4 shows an example specimen of each species, and the differences are circled. The pms is curved dorsally in *U. stansburiana*, and as a result, the anterior most tooth also curves dorsally. The pmp of *U. ornatus* has a distinct notch in the medial region. *U. stansburiana* has a similar notch in their pmp, but it occurs in the anterior region, caudally to the posterior most tooth. Furthermore, the thin-plate spline shows transformation in these characters when comparing the mean maxilla shape of *U. ornatus* and *U. stansburiana* (Fig. 5). These features are considered to be apomorphies and can be used to distinguish one species from the other.

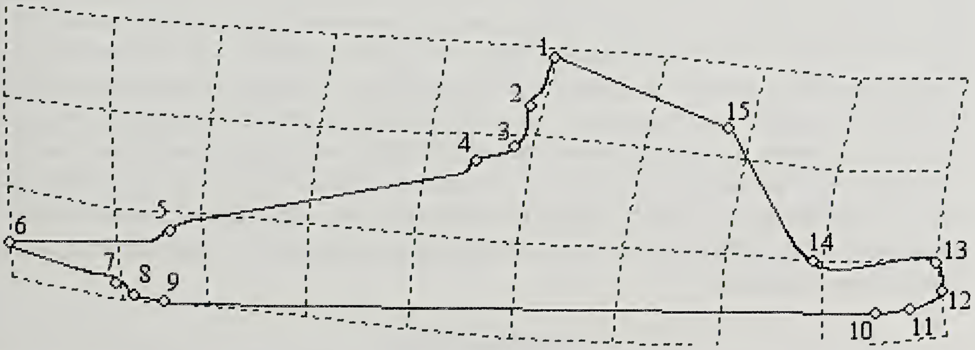

Fig. 5. Thin-plate splines showing the differences in mean maxilla shape. *Urosaurus ornatus* consensus has been morphed into the *Uta stansburiana* consensus.

Other characters selected as significant by the stepwise DFA were: 1) height of the posterior maxilla process tip, and 2) height of the lacrimal/maxilla suture process tip. These characters have lower Wilk's Lambda values, and noticeable differences between species are not apparent in every specimen observed. The pmp tip is curved dorsally in *U. ornatus*; however, this feature is not always consistent. Height of the lmsp varied greatly amongst all specimens, but the process appears to be slightly higher in *U. ornatus*. Additionally, height of the lmsp is the only significant character to have a low loading score for all eight components.

At first glance, *U. ornatus* might seem very different from *U. stansburiana*, for example, *U. stansburiana* does not have a visible pfmssp, while *U. ornatus* does (Fig. 4). It is important to note that this is not consistent and therefore is not a good character to use for identification. Also, *U. stansburiana* appears to have a clear differentiated nr from the dms, however this is also inconsistent amongst specimens. In *U. ornatus*, the lmsp is more pronounced and there exists a small process between the pfmsip and the lmsp, but these traits are also inconsistent, and therefore should not be used for identification.

There are a few characters that were not selected by the stepwise DFA that may seem useful because they are associated with the pms: the height of the ventral edge of the pms and the height of the anterior base of the anterior most tooth. Even if these characters showed a significant difference between species, they were possibly not selected as significant due to variation within a species, thereby failing the tolerance test. We conducted only a stepwise DFA because we wanted significant characters that were also consistent and showed little to no variation within a species. Characters that meet these criteria are considered apomorphies, and can be used to identify fossils.

The majority of the significant characters were along the Y axis, implying height differences in the maxilla, which could result in height differences in the face. Based on the observations of each specimen, *U. ornatus* has a taller face, whereas *U. stansburiana* has a short and squat face. The difference in face shape matches what is known about the biology of each lizard; *U. ornatus* is typically found on trees, while *U. stansburiana* is on the ground and hides under rocks (Stebbins 2003).

Conclusions

Despite past difficulties in identifying the two phrynosomatids *Urosaurus ornatus* and *Uta stansburiana*, there is a statistical difference when comparing the maxilla bone morphology. Three reliable characters can be used when distinguishing the maxilla of *U. ornatus* from *U. stansburiana*: 1) ventral edge of the premaxilla/maxilla suture height, 2) ventral notch on the posterior maxilla process height, and 3) posterior base of the anterior most tooth height. Since these character differences are observable in each specimen, they are considered apomorphies and can be used for fossil identification. Other less-reliable characters that have potential for identification are: 1) posterior maxilla process tip height, and 2) lacrimal/maxilla suture process tip height. These data are important for fossil identification because the maxilla is a common bone in the squamate fossil record and taxonomically significant characters are still unknown for several groups. Even though this study only examines two species, these results are encouraging and will hopefully result in similar studies using more taxa. It is important to continue morphometric analyses on different species and cranial elements for a more comprehensive guide to identify fossil squamates.

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The Effects of a Prolonged Drought on Southern Steelhead Trout (*Oncorhynchus mykiss*) in a Coastal Creek, Los Angeles, California

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Abstract.—Long-term lifecycle monitoring of federally endangered southern steelhead trout (*Oncorhynchus mykiss*) in Topanga Creek provides a unique opportunity to examine the health and abundance of a steelhead population before (2008–2011) and during (2012–2016) a prolonged drought. We found that the five-year drought resulted in a substantial and significant decline in available wetted habitat suitable for rearing and upstream migratory access for anadromous adults. The response of the steelhead population has been a significant reduction in anadromous spawning, distribution of rearing, and abundance of all life stages of anadromous and resident steelhead. After five years of drought a population that exceeded 325 individuals in 2008, now numbers fewer than 50 fish, and appears to be at extremely high risk of extirpation. Acknowledging the possibility of increased drought regionally and globally, the need to bolster southern steelhead resiliency to additional disturbance is paramount.

Southern steelhead trout (*Oncorhynchus mykiss*) are an endangered species, with an estimated population of less than 500 anadromous adults in California watersheds from Santa Barbara County south to the Mexican Border (NMFS 2012). Adapted to an intrinsically high disturbance environment, the life history trajectory of southern steelhead trout is extremely variable, and includes both resident and anadromous fish (NMFS 2012). The two genetically indistinguishable behavioral forms occur in the same watersheds in southern California, so this study refers to both forms as *O. mykiss*, unless otherwise noted. Threats in this region are high from both anthropogenic (fish passage barriers, habitat loss, water quality, etc.) and natural factors, like drought and wildfires (NMFS 2012). In prolonged periods of drought, flows may become insufficient to support upstream migration of adults from the ocean to freshwater spawning habitat during winter, and to support downstream migration of juveniles during spring. Drought conditions can impact juvenile rearing by preventing or restricting access to preferred habitats, and direct mortality at all life stages can occur when low flows isolate fish in disconnected or dewatered habitats, subjecting them to predation or stranding. Lower flows may also decrease invertebrate production and drift, thus reducing available food supply and negatively affecting growth (Harvey et al. 2006, Hakala and Hartman 2004, Canton et al. 1984). Despite the clear mechanism by which drought can impact salmonid populations, there are few long-term studies documenting the population level responses of salmonids to either direct or indirect effects of prolonged drought (Matthews and Marsh-Matthews 2003).

Topanga Creek has been a focal creek for lifecycle monitoring of *O. mykiss* since 2008. The small population occupying the creek was extirpated for almost 20 years between the drought of the late 1970's and re-establishment in 1998 (Bell et al. 2011a). The nine years of comprehensive monitoring and analysis of abundance, distribution, habitat suitability, and growth since 2008 provides a unique opportunity to closely examine the changes in this population in response to the recent California drought. In the Mediterranean winter-wet and summer-dry climate characteristic of southern California, seasonal drying of stream reaches is common, particularly when rainfall during the previous winter was normal or less than normal (Meixner and Wohlgemuth 2001, Dallas 2013). However, the recent five-year drought evolved from classification as ‘abnormally dry’ in 2012, to ‘severe’ in 2013, ‘extreme’ in 2014, and increased to ‘exceptional drought’ for all of 2015–2016 in the Santa Monica Bay (US Drought Monitor 2016). For the purposes of this study, “before drought” is classified as the period from 2008 through 2011, and the period of “drought” is classified as 2012 through 2016. Here we examine how this multi-year drought affected habitat conditions, abundance, and distribution for the Topanga Creek population of *O. mykiss*.

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Materials and Methods

Topanga Creek drains a 50 km^2 coastal watershed into the Santa Monica Bay, entirely within Los Angeles County. Approximately 37 km^2 of the watershed is dedicated public open space, and the remaining area is privately held land. Distances upstream from the ocean within Topanga Creek are referred to as river kilometers (rkm). The study area (Fig. 1) extends from the ocean at Topanga Beach (0 rkm) upstream to the natural limit of anadromy (5.3 rkm). This represents both the current and documented range of *O. mykiss* from initial records in the 1930’s to present in Topanga Creek. The study area is divided into two reaches. The lower reach (0–3.6 rkm) has a gradient between 0–3% and is characterized by alluvial floodplain and mixed riffle, runs and step pools, with 14 mid-channel pools that remained watered and with stable depth through multiple years of drought up to 2016, when much of the reach dried down to subsurface flows uninhabitable by *O. mykiss*. The upper reach (3.6–5.3 rkm) gradient ranges from 3–6%, with 16 boulder-dominated step pools, bedrock pools and mid-channel pools that remained wetted throughout the study period. There are no tributaries in the watershed that can support *O. mykiss*.

Long-term monitoring methods conducted in Topanga Creek have been previously described in Bell et al. (2011b) and Dagit et al. (2015).[1] Below we provide a summary of the key methods applied in analysis of the observed effects of the recent drought on steelhead habitat quality and population.

To characterize rainfall during the pre-drought and drought period, precipitation was measured by Los Angeles County Department of Public Works (LACDPW) gauge #318 located at the Topanga Fire Station in the center of the watershed (Fig. 1). Data is summarized annually as a water year (October 1 through September 30). Flow in Topanga Creek was recorded by a Los Angeles County stream gauge (LACDPW F54C) located in the lower main stem at 3.6 rkm (Fig. 1). This gauge was intermittently functional during the study period due to low flows and sediment buildup that isolated the gauge from the thalweg but was functional during high flows. Therefore, flow monitoring in Topanga Creek was used to assess anadromous steelhead migration opportunities that occur during high flows, but was not considered a reliable metric for characterizing average or low flows.

To describe stream habitat within Topanga Creek before and during the drought, habitat characteristic data including habitat type and river kilometer were measured and recorded

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[1] Dagit, R., K. Adamek, S. Albers, E. Montgomery, and A. Sanchez. 2015. Topanga Creek Steelhead Monitoring March 2011–December 2014. Prepared for CDFW Contract No. P1050009. Available from: info@rcdsmm.org, RCD of the Santa Monica Mountains, 540 S. Topanga Canyon Blvd., Topanga, CA.

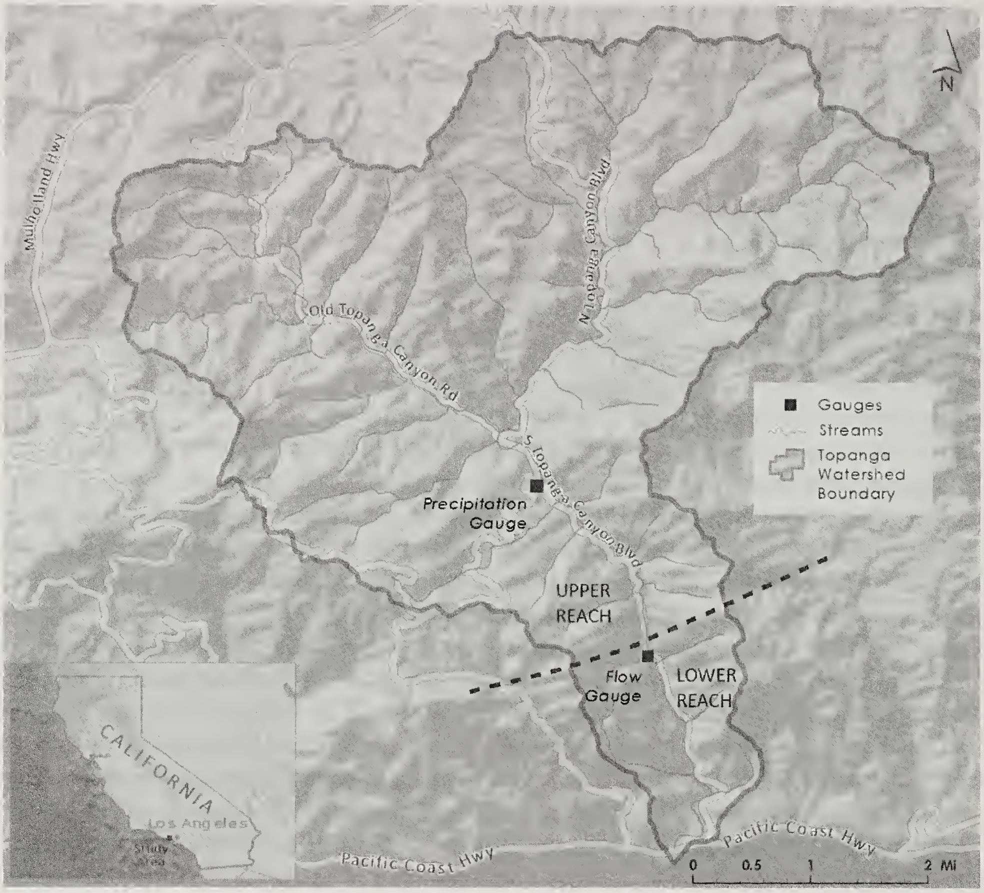

Fig. 1. Map of study reaches within the Topanga Creek study area (0–5.3 rkm)

during monthly surveys following the methods of Flosi and Reynolds (updated 2010). Pool habitat unit area and volume were estimated based on pool length, width, and average water depth measurements. Assessment of pool area and pool volume was conducted within 30 refuge pools (described below) to assess trends. Habitat characterization also included documentation of the proportion of dry habitat units. For analysis, data from the driest period of the year (July through September) was assessed to represent the most critical conditions for rearing and recruitment of young of the year *O. mykiss*.

To assess the abundance of *O. mykiss* within Topanga Creek before and during the drought, snorkel surveys were conducted monthly within all wetted habitat in the study area. Numbers of observed *O. mykiss* within individual habitat units were recorded for three size classes: young-of-year (<10 cm fork length [FL]), juvenile (10–25 cm FL), and adult (>25 cm FL). Data on redd location and size (length, width, depth, and substrate size) were recorded according to the redd survey protocol developed by NMFS (2010).

Conditions during the snorkel surveys were highly variable, and the amount of wetted habitat varied substantially as dry down occurred during the drought. To assess trends in observed abundance independent of shifts in wetted habitat, a subset of 30 pools (14 in the lower reach, 16 in the upper reach) were selected for targeted monitoring. These pools were continuously wetted even during the driest conditions observed, with the exception of four pools in the lower reach which experienced dry down in 2016. These 30 “refuge” pools were surveyed monthly for *O. mykiss* observed abundance, and analyzed separately from the comprehensive snorkels surveys (which included the entire study reach), to assess trends in observed abundance independent of wetted habitat.

To assess growth rates and migration patterns of *O. mykiss* before and during drought, a total of twelve Passive Integrated Transponders (PIT) tag mark-recapture events were held in November of 2008–2016, and March of 2011–2013. During each event, all wetted habitat units were sampled with one pass using two backpack electrofishers. Captured fish were anesthetized with MS-222, scanned with a hand-held PIT tag reader, and fork length was measured to the nearest millimeter with a wetted fish measuring board. New captures were also tagged before being released upon recovery in their pool of capture. A more detailed description of these methods is found in Dagit and Krug (2016).

Analysis consisted of exploring relationships between environmental descriptions of the drought (rainfall, fraction of dry habitat units, pool volume, pool area), and population metrics (observed abundance, spatial distribution) of *O. mykiss* before (2008–2011) and during drought (2012–2016). Conditions were further assessed based on annual precipitation as well as precipitation during the lowest-flow period of the year (average of the July, August, and September) for each year. Abundance of *O. mykiss* of was based on redd counts, number of *O. mykiss* observed in all units surveyed during monthly snorkel surveys, and by the subset of the population within the 30 refuge pool units. Analyses were made using the average values of abundance across all months of the calendar year, and average values for the lowest-flow period of the year (averaging July, August, and September).

Results

Precipitation before drought averaged 54.56 cm (21.48″), and was substantially higher than the 25.12 cm (9.89″) annual average during the drought (t-test; $p < 0.01$; Table 1). Consequently, average pool area of the 30 refuge pools declined substantially in the drought period (t-test; $p < 0.01$; Fig. 2), as did average pool volume (t-test; $p < 0.05$; Fig. 3). With the decline in precipitation, the percentage of the study area that was dry July-September before drought (32%) increased significantly (t-test; $p < 0.05$) during the drought 46%. The lower reach of Topanga Creek (with corresponding lower gradient, 0–3.6 rkm) experienced seasonal dryness to some extent in all years, but the drought increased the length (both spatially and temporally) of low flow or sub-surface flow conditions (Fig. 4). The upper creek (upstream of 3.6 rkm) did not have dry sections, but did experience lower pool volume and flow conditions in drought.

Drought and creek condition metrics were strongly correlated. Rainfall was a good predictor of how long the seasonally dry sections would remain dry ($R^2 = 0.75$, $p = 0.006$) as well as how much of the reach would have dry patches ($R^2 = 0.76$, $p = 0.006$) (Fig. 4). Some of the areas that remained wetted were likely sustained by groundwater input from a variety of seeps and springs located throughout that reach (Tobias[2] 2006). The frequency and magnitude of high-flow events declined during 2012–2016 (Fig. 5). From 2008–2016, the longest period of potential anadromous migration (adults or smolts) was for two days in February 2010 and March 2011. Between 2013 and 2016 there were fewer than five days total with sufficient flows (greater than

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[2] Tobias, V.D. 2006. Groundwater sources and their influence on the distribution of steelhead in Topanga Creek, Topanga, California. Master’s thesis. University of Michigan, Ann Arbor.

Table 1. Summary of environmental conditions and response of *O. mykiss* before drought (2008–2011) and during drought (2012–2016) in Topanga Creek, California.

	t-test (one-tailed, homoscedastic)		
	Before drought 2008–2011	Drought 2012–2016	p-value
Drought metrics			
Jul-Sep dry (% of study area)	32	46	0.022*
Rainfall (inches)	21.48	9.89	0.007**
Jul-Sep pool area (m^2)	5739.83	3973.01	0.008**
Jul -Sep pool volume (m^3)	372185.08	278057.09	0.028*
Spawning activity			
Redd counts	4.00	1.60	0.044*
Jul-Sep average abundance: study area			
Young of the year (length $\leq$10 cm)	155.00	37.60	0.031*
Juvenile (length 10–25 cm	91.08	26.20	0.019*
Adult (length $\geq$25 cm)	17.58	8.40	0.006**
All	263.67	72.20	0.010*
Jul - Sep average abundance: thirty pools			
Young of the year (length $\leq$10 cm)	52.63	12.60	0.038*
Juvenile (length 10–25 cm	45.04	14.33	0.012*
Adult (length $\geq$25 cm)	10.04	4.80	0.009**
All	107.71	31.73	0.006**

*$p < 0.05$.
**$p < 0.01$.

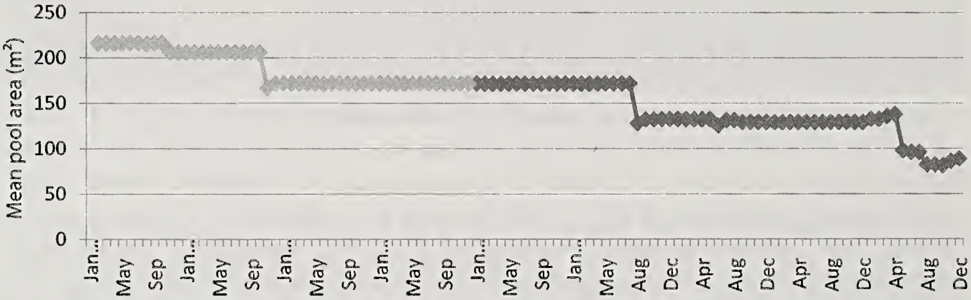

Fig. 2. Mean pool area within study area before (2008–2011) and during (2012–2016) drought in Topanga Creek.

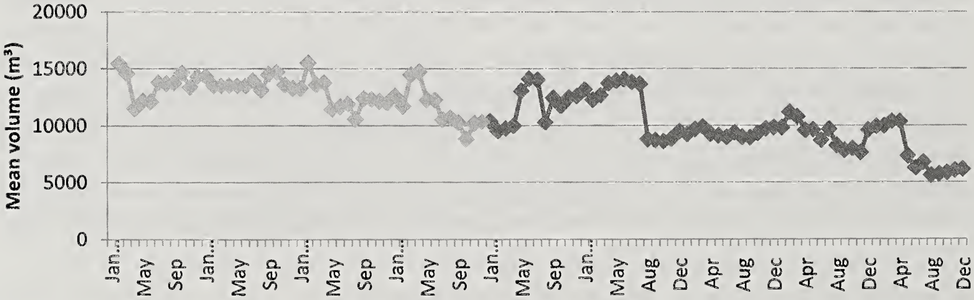

Fig. 3. Mean pool volume within study area before (2008–2011) and during (2012–2016) drought in Topanga Creek.

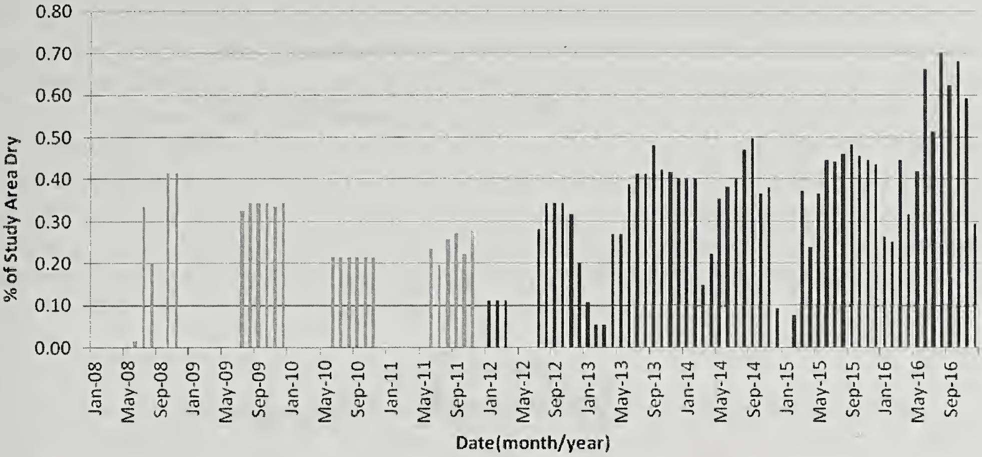

Fig. 4. Percentage of study area that was dry before (2008–2011) and during (2012–2016) drought in Topanga Creek.

100 cfs mean daily flow) to connect habitat and provide anadromous fish passage for adults or smolts (RCDSMM unpublished data).

The average number of observed *O. mykiss* in July through September significantly declined from before drought (263 individuals) to drought years (72 individuals, t-test; $p < 0.01$) throughout the study area (Table 1). Declines were significant for all age classes, most substantially for adults, which declined from an average of 18 adults before drought, to eight adults on average during the drought (t-test; $p < 0.01$). Fewer observations of *O. mykiss* during drought was also apparent when analysis focused on the 30 refugia pools. There was a significant decline in

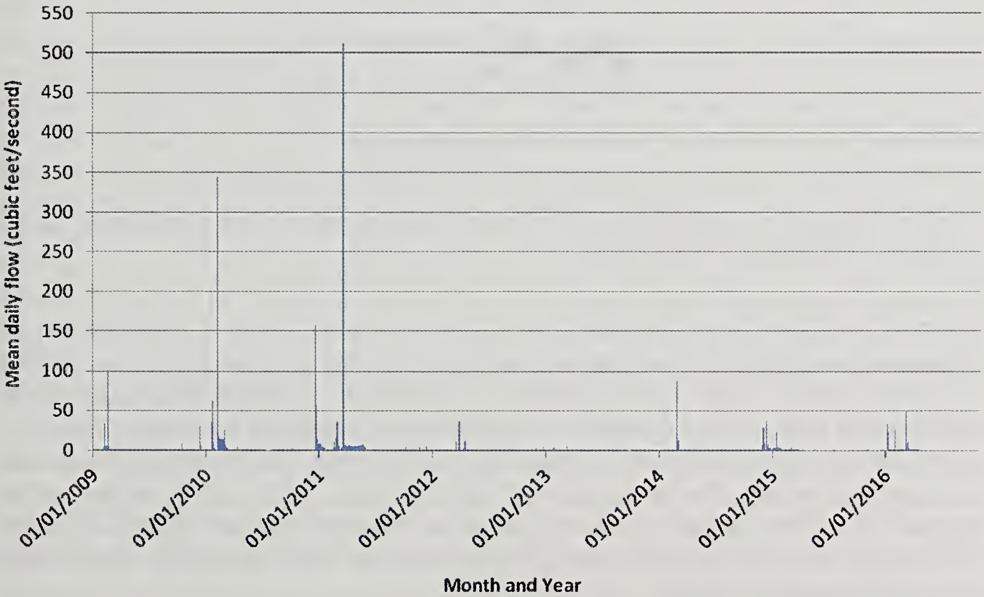

Fig. 5. Flow measurements in Topanga Creek during high flow events (cfs) at F54C-R. Provided by Los Angeles County Department of Public Works.

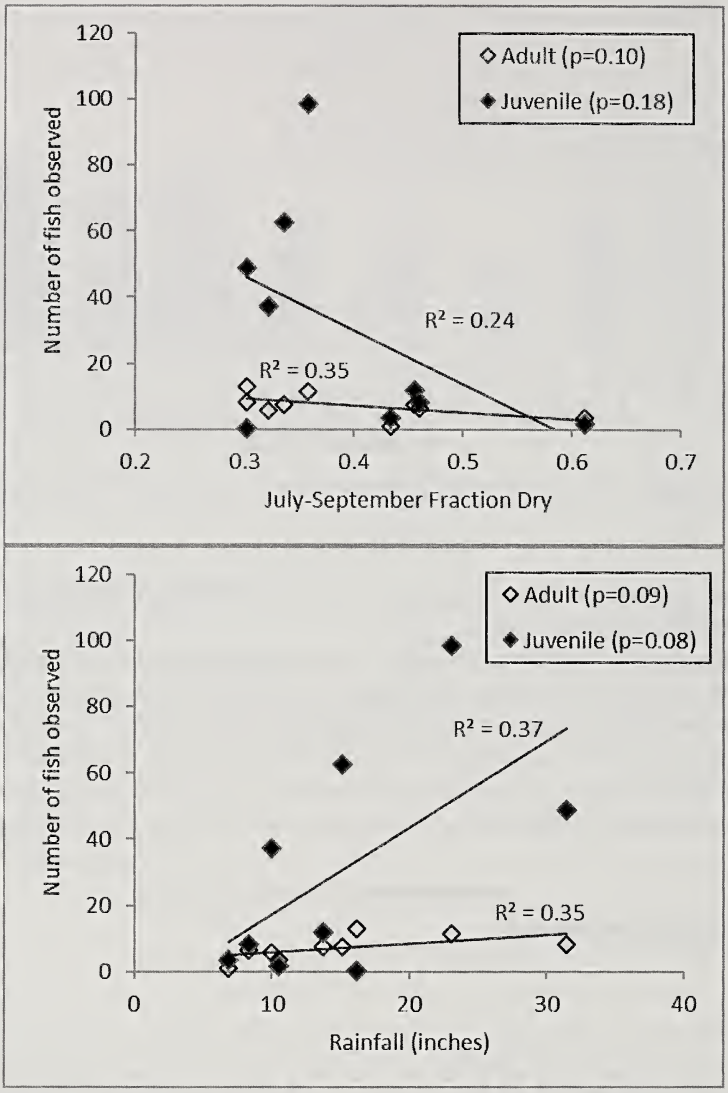

Fig. 6. Observed *O. mykiss* abundance in 30 refuge pools during July, August, and September surveys compared to creek drying and annual rainfall.

observed abundance for all three age classes of trout combined (t-test; $p < 0.01$). Observed abundance was negatively correlated with the fraction of dry units, and positively correlated with annual rainfall, though neither correlation was statistically significant (Fig. 6). Overall, the abundance of young-of-year *O. mykiss* was significantly lower during the drought (t-test; $p < 0.038$; Table 1). The total number of observed *O. mykiss* redds was low prior to the drought (<5), and declined significantly during the drought (t-test, $p < 0.05$), with no redds observed during 2015 or 2016. A single anadromous adult was observed each year of 2008, 2010, and 2012; but based on redd size and presence of few anadromous adults, the majority of redds were produced by resident *O. mykiss*.

Distribution of *O. mykiss* in Topanga Creek was normally seasonally affected by low flow barriers and impediments to migration before drought, but loss of surface flow measured during snorkel surveys expanded during the drought. From 2008–2011 many of the passage impediments were still passable by fish moving downstream even under low flow conditions, however as the drought continued, flows decreased and wetted habitat contracted making movement difficult either up or downstream except during rain events. Overall, the remaining fish re-distributed to the remaining available habitat as portions of the stream dried up. Thus, the number of habitat units observed to be occupied by *O. mykiss* decreased substantially during the drought from an average of 55 habitat locations before the drought to 33 habitat locations during the drought (t-test; $p < 0.01$; Table 1). The distribution of redds also shifted upstream of 3.6 rkm as the dry downs below 3.6 rkm expanded, concentrating them into remaining wetted habitat upstream.

Discussion

Seasonal droughts are a recurrent and defining feature of Mediterranean climate streams, with predictable reductions in flows during the dry summer and fall months (Lake 2011). *Oncorhynchus mykiss* populations are adapted to regular reductions in stream flows, and have historically persisted and thrived within their southern range (NMFS 2012). However, the results of this study indicate that a prolonged drought severely limited available habitat for *O. mykiss*, with a subsequent negative impact on anadromous spawning, opportunity for smolt migration, and total observed abundance of all life stages.

While the significant loss of surface flows and wetted available habitat reported in this study have a direct impact on *O. mykiss* abundance, the synergistic ripple effects of other elements associated with drought such as habitat type conversion, decreased water quality, potential changes to stream thermodynamics, reduced abundance of benthic macro-invertebrate food sources (Garcia et al. 2015, Matthews and Marsh-Matthews 2003, Montgomery et al. 2015) also likely contributed to the significant decline in numbers of observed *O. mykiss*. Habitat type conversion from runs to riffles, and riffles to patches of emergent vegetation, reduced available suitable spawning, rearing and holding refugia (Resource Conservation District of the Santa Monica Mountains (RCDSMM) unpublished data). Habitat quality was compromised by reduced volume in the refugia pools. By August 2016, it was necessary for the California Department of Fish and Wildlife (operating under a permit from National Marine Fisheries Service) to relocate three individuals ranging in size from 10 – 30 cm FL due to stranding in evaporating pools with dissolved oxygen levels below 2 mg/l (RCDSMM unpublished data). It appeared that groundwater sources ameliorated the effect of reduced surface flows on water temperature to some extent, such that maximum and average summer temperatures did not increase during the drought (Montgomery et al. unpublished). However, the minimum temperatures steadily rose during April and May over the drought years and eventually exceeded 15°C, the critical threshold identified by Myrick and Cech (2005) for *O. mykiss* egg incubation and emergence. Our results were not able to discern if this increase in minimum temperatures impacted egg viability or spawning success, but few redds were observed, and fry production was severely limited during the drought.

Previous research on the population of *O. mykiss* in Topanga Creek by Bell et al. (2011a) focused on population factors that supported their long-term persistence in this small creek with high disturbance regime. The conceptual model that resulted from this research suggested that the most significant limiting factors for the population were associated with limited migration opportunities for smolts to reach the ocean, and anadromous adults to return to the creek to spawn (Bell et al. 2011a); both factors which are strongly affected by drought. In Topanga Creek, rate of reproduction does not appear sufficient to seed available rearing habitat. Analysis of age class response using July – September average values highlight the loss of young of the year and low recruitment as the drought intensified (Table 1). The lack of young of the year in 2011 appeared to be related to a strong storm event in March of that year when snorkel surveys revealed that the numbers of smolt size *O. mykiss* dropped abruptly (RCDSMM unpublished data). The small increase observed in 2015 reflects successful recruitment from three resident redds found in 2014.

Because adult anadromous steelhead fecundity (usually >3,000 eggs per female) is much greater than that of resident female *O. mykiss* (usually <1,000 eggs) (Moyle 2002), population dynamics are potentially very different in years when anadromous individuals spawn versus years in which only resident *O. mykiss* spawn. Therefore, one of the most significant effects of the drought was likely the dramatic reduction in days when the lower reach of the study area received sufficient flows to support anadromous migration. Consequently, during the drought there was no anadromous spawning, as well as limited resident spawning, and thus very low levels of fry production.

Lagoon conditions were not analyzed in this paper, but would have a strong influence on the potential opportunities for anadromy as well. Topanga lagoon is currently 0.72 hectares of wetted area constrained by fill banks on the east and west, with only a 24 m opening under the Pacific Coast Highway bridge. There is little wetland vegetation and extremely limited instream cover for fish. Lagoon rearing habitat for juvenile *O. mykiss* migrants preparing to smolt has been demonstrated to be critically important for California coast steelhead populations. Significantly higher growth rates and ocean survival by steelhead that reared in lagoons has been documented, even with lagoon water temperatures as high as 24°C (75°F) (Smith 1990[3], Hayes et al. 2008, Bond et al. 2008). Depending partly on growing conditions in their rearing habitat, steelhead may migrate downstream to estuaries as age 0+ juveniles or may rear in streams for up to four years before outmigrating to the estuary and ocean (Shapovalov and Taft 1954). Ocean connectivity, as well as up and downstream movement were severely limited between the lagoon and the creek, reducing the life history diversity to resident only individuals.

Food for *O. mykiss* in Topanga Creek documented before the drought by gastric lavage was dominated by dipterans, tricoperans and baetids (Krug et al. 2012). There are numerous studies that document the response of BMI communities to drought (Hall et al. 2016, Stillwater 2007). In Topanga Creek Montgomery et al. (2015) found a significant shift from a baetid dominated community to a chironomid dominated community in low rainfall years, with extremely low numbers overall. Therefore, we expected to see a reduction in growth rates for the Topanga Creek population during the drought. We observed that growth rates declined slightly during the drought, but were not significantly different than those observed prior to drought conditions. This suggests that even with more restricted habitat available, and a potentially different suite of food organisms available, the fewer number of fish (and thus lower density) were still able to find sufficient food and continue to grow.

Following the drought, the population in 2016 numbered fewer than 50 individuals, with approximately 10 resident adults, and no anadromous spawning. These low numbers paired with spatial isolation could potentially cause a severe genetic bottleneck in the population. A severe reduction in, or extirpation of the Topanga Creek population has substantial implications for the entire Southern California steelhead meta-population as well. Analysis indicates that the *O. mykiss* in Topanga Creek are genetically distinct from other populations and have little influence from historical hatchery introductions (RCDSMM unpublished data). The long-term recovery of the southern California steelhead trout throughout their range relies on genetic intermixing that is only possible with sufficient smolt production, and migration opportunities in source watersheds (Boughton et al. 2006), especially since increased resiliency to climate change may require specific genetic adaptations that could occur in independent populations like Topanga Creek (NMFS 2016, Clemento et al. 2009). However, the loss of migratory opportunity documented here in the 2012 to 2016 Topanga Creek *O. mykiss* because of drought induced loss of habitat connectivity and population abundance prevents genetic mixing with the meta-population.

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[3] Smith, J. J. 1990. The effects of sandbar formation and inflows on aquatic habitat and fish utilization in Pescadero, San Gregorio, Waddell and Pornponio Creek Estuary/Lagoon systems, 1985–1989. Dept. Bio. Sci., San Jose State University, San Jose, California.

Although it is challenging to assign the decline of *O. mykiss* relative abundance in Topanga Creek solely to drought (i.e., overall numbers of individuals were low before the drought), it is evident that the increased loss of habitat connectivity and migration opportunities poses a substantial threat. This genetically distinct population segment possesses a unique diversity of adaptations that has permitted them to survive the erratic and unpredictable climate conditions in southern California for millennia, but the cumulative impact of both anthropogenic and natural stressors has brought the population to the brink of extinction (NMFS 2012). The most recent five-year drought highlights the tenuous condition of these small populations in coastal creeks, with the decline in relative abundance observed in Topanga Creek being just one example. This population blinked out in response to drought in the 1980's (Bell et al. 2011b), but at that time there were more straying anadromous adults to re-establish the population when habitat connectivity was available. NMFS (2016) concluded that the drought has increased the threat level to the already endangered population, and recommends the prevention of local extirpations of steelhead populations. Restoring wetland function and habitat quality of the degraded lagoon habitat in Topanga Creek watershed could potentially support *O. mykiss* recovery and resiliency both locally and regionally by facilitating smolting and providing greater opportunity for fish passage and anadromous recruitment.

Conclusions

Long-term monitoring of the Topanga Creek population of *O. mykiss* presented a unique opportunity to assess the impacts of a prolonged five-year drought in a southern California coastal stream. We found that below average rainfall during five years of drought resulted in too few substantial flow events to provide habitat connectivity and support anadromy. The proportion of wetted habitat significantly declined, as did the total number of habitat units available to support *O. mykiss*. No anadromous spawning occurred and resident spawning also significantly decreased during the drought period. Abundance of all life-stages of *O. mykiss* in Topanga Creek significantly declined throughout the study reach and within monitored refuge pools, but growth rates of individuals in those pools declined only slightly. Continued monitoring of the Topanga Creek population is highly recommended to further clarify the long term impacts of the drought, and/or to monitor the recovery of the population from this chronic disturbance.

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A Longitudinal Temperature Profile of the Los Angeles River from June through October 2016

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Abstract.—This pilot study developed a longitudinal temperature profile of the Los Angeles River by deploying temperature loggers throughout the watershed between June and October 2016. The watershed was divided into zones based on river system component, urbanization, and channelization. Channelized sites recorded the highest temperatures, tributaries recorded the lowest, and the estuary showed the most fluctuation. Overall, temperatures were too warm to support re-introduction of native fish but currently support non-native fish species. Temperature mitigation is needed for native species to re-establish. Albeit limited in scope, this study establishes a baseline of summer/fall temperatures in the Los Angeles River.

The 82-kilometer-long Los Angeles River (LAR) is an urban river that flows through 14 cities and unincorporated areas in Los Angeles County, California. Approximately 77.25 km of the 82 km main stem of the river is contained in concrete flood control channels, leaving three miles of river with natural channel bottom along the main stem. The soft bottom reaches occur at three locations: the estuary in Long Beach between Willow Street Bridge and the Long Beach Harbor, the Sepulveda Flood Control Basin, and the Glendale Narrows. Tributaries in the upper watershed within the Angeles National Forest, upper Arroyo Seco and Upper Tujunga Wash, remain in a fairly natural state with natural substrate and riparian vegetative cover. When these reaches flow into more urbanized areas, however, they are often channelized as well, with variable levels of natural channel bottom and riparian vegetation remaining depending on flood risk to nearby urban areas.

Currently, native fish species only reside in the upper reaches of the watershed at Big Tujunga Wash and the Arroyo Seco, as well as in the estuary. The obligate freshwater community found in the upper reaches includes arroyo chub (*Gila orcutti*), Santa Ana speckled dace (*Rhinichthys osculus* ssp.), and Santa Ana sucker (*Catastomus santanae*). The freshwater life history form of rainbow trout (*Oncorhynchus mykiss*) is also present in the upper watershed in the Arroyo Seco, but the federally endangered anadromous southern steelhead form of *Oncorhynchus mykiss* was last observed in the LAR watershed in the 1940s (Swift et al. 1993). The Recovery Plan for the extirpated unarmored threespine stickleback (*Gasterosteus aculeatus williamsoni*) calls for reintroduction in the LAR watershed[1], while the now state and federally listed endangered Pacific lamprey (*Entosphenus tridentatus*), which was historically found in rivers throughout

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[*] Corresponding author: rdagit@rcdsmm.org

[1] US Fish and Wildlife Service. 1985. Unarmored threespine stickleback recovery plan. USFWS Portland, Oregon.

southern California, has not been observed in the LAR in many years[2]. Currently, numerous non-native fish species, including common carp (*Cyprinus carpio*), Nile tilapia (*Oreochromis niloticus*), green sunfish (*Lepomis cyanellus*), and largemouth bass (*Micropterus salmoides*) are found in the limited soft-bottom areas of the watershed and represent the dominant ichthyofauna of the river reaches that are targeted for major restoration efforts[3,4].

The Los Angeles River is headed for an extraordinary restoration effort[5], but the form and direction of restoration is still under development. Underpinning restoration of the river is the need to understand how the contemporary aquatic community will respond to restorative actions, and to identify barriers to re-establishing native species. Without accurate characterization of the existing instream conditions in priority restoration reaches, the benefits of the multi-billion-dollar effort to revitalize the river will be difficult to determine.

Among the suite of factors that influence distribution and abundance of fish species, water temperature is one of the most important. As ectotherms, the body temperature of a fish is linked to the temperature of the water in which it resides. This means that growth, metabolism, feeding rate, reproduction, and rearing are all tied directly to water temperature. Furthermore, most aquatic organisms, such as benthic macroinvertebrates, that fish rely upon as food sources are poikilotherms, and are also limited by water temperature.

Data on critical thermal temperatures for native fishes historically found in the LAR watershed are limited in the current literature. While increased summer water temperatures tend to be a major limiting factor for most salmonids in other areas, multiple studies conducted in southern California show that rainbow trout (*O. mykiss)* demonstrate more flexibility in their temperature range and an ability to acclimate to higher temperatures within the southern extent of their range (Boughton et al. 2007; Myrick and Cech 2000; Myrick and Cech 2005; Spina 2007). Critical thermal maxima (CTM) ranging from 23°C to 31.5°C have been reported for *O. mykiss* in southern California creeks (Bell 1986; Dagit et al. 2009; Sloat and Osterback 2012). A detailed study of the unarmored threespine stickleback (*G. aculeatus williamsoni*) in the Santa Clara River found CTM for this species was 30.4°C when individuals were acclimated to 8°C, and 34.6°C when acclimated to 22.7°C (Feldmeth and Baskin 1976). Unfortunately, among historically native LAR fishes, these are the only species for which detailed experimental studies on CTM have been published.

While not experimentally derived, field observed temperatures from studies of native fish in the Los Angeles basin and other southern California watersheds can be utilized as indicators of the thermal requirements of target species relative to the conditions currently found in the LAR. For instance, field observations of Santa Ana sucker (*C. santanae*) published by Feeney and Swift (2008) show that larvae may bask in slower flowing areas where temperatures reach 24°C, while juveniles may retreat from warm summer flows (up to 30°C), congregating in cooler areas (15–22°C) near tributary or groundwater sources. Saiki et al. (2007) observed juvenile Santa Ana suckers in June in the Santa Ana River when daytime temperatures averaged 25.3°C, and ranged to 30.8°C, as well as in September in the San Gabriel River when temperatures averaged 19.6°C (range 15.0–22.9°C). USFWS[6] reported mortality events for Santa Ana suckers when temperatures exceeded 32.8°C in the Santa Ana River and 26.7°C in Big Tujunga Creek.[6] In a survey of the upper San Gabriel River from 2007 and 2008, O'Brien et al. (2011) reported mean daily temperatures of ~21°C in the north and east forks of the San Gabriel River and ~20°C in the west fork. This study reported Santa Ana sucker, rainbow trout, and Santa Ana speckled dace in all three forks of the San Gabriel River, while arroyo chub were only found in the east and west forks (O'Brien et al. 2011). While arroyo chub are physiologically adapted to survival in habitats with wide temperature fluctuations (Castleberry and Cech 1986), they are most commonly found in low gradient streams where water temperatures do not exceed 28°C, and where spawning temperatures ranging from 14–22°C are available (O'Brien 2009; Moyle et al. 2015). Moyle et al. (1995) found that Santa Ana speckled dace prefer perennial streams fed by cool springs that maintain summer water temperatures below 20°C.

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Even though much of the LAR has been channelized, there are still areas with natural substrate that could potentially provide suitable habitat for native fish (i.e. Glendale Narrows, Sepulveda Basin). The lack of concrete lining at these locations accommodates groundwater upwelling, which provides refugia habitat that currently support both non-native fishes as well as native amphibians absent in concrete reaches of the LAR[7]. Since water temperature is so closely tied to the distribution and abundance of fish species at various life stages and with that of their prey animals, a longitudinal temperature profile of the river can be used as an indicator of habitat quality on the watershed scale (Poole et al. 2001a). Determining where water temperature in the LAR is currently suitable for native fish is an important first step for any proposed restoration effort. If temperatures are in fact suitable for native species, then future efforts can focus on targeted in-stream and riparian habitat restoration, non-native species management, or other non-temperature related actions. If temperatures in the river are not suitable for native species, future restoration efforts should be developed with a focus on improving the temperature regime of the river for native fishes.

A study to capture a detailed thermal profile of the LAR was initiated in early 2016, with installation of continuously recording temperature data loggers at 13 sites throughout the watershed. Temperature data was recorded from June through October 2016. The intent of the study was threefold: to characterize temperatures throughout the watershed; to document current baseline conditions at representative locations during the most stressful summer conditions; and to identify opportunities for restoration of native fish habitat. While limited in scope, the present study provides an initial, albeit incomplete, picture of baseline summer/fall temperatures in the LAR against which future studies and conditions can be compared.

Materials and Methods

The study area includes the main stem and three major tributaries of the LAR, from its headwaters in the Angeles National Forest and western San Fernando Valley, to the estuary in Long Beach (Fig. 1). For comparison purposes, the watershed is divided into six zones based on river component (tributaries: A, C, E; mainstem: B, D, and estuary: F). Tributaries within

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[6] US Fish and Wildlife Service. 2014. Draft recovery plan for the Santa Ana sucker. USFWS Pacific Southwest Region, Sacramento, CA.

[7] Swift, C.C. and J. Seigel. 1993. The past and present freshwater fish fauna of the Los Angeles River, southern California, with particular reference to the area of Griffith Park. in The biota of the Los Angeles River: an overview of the historical and present plant and animal life of the Los Angeles River drainage. (K. Garrett, ed.) Los Angeles Natural History Museum Foundation, Los Angeles, CA, 28 pp.

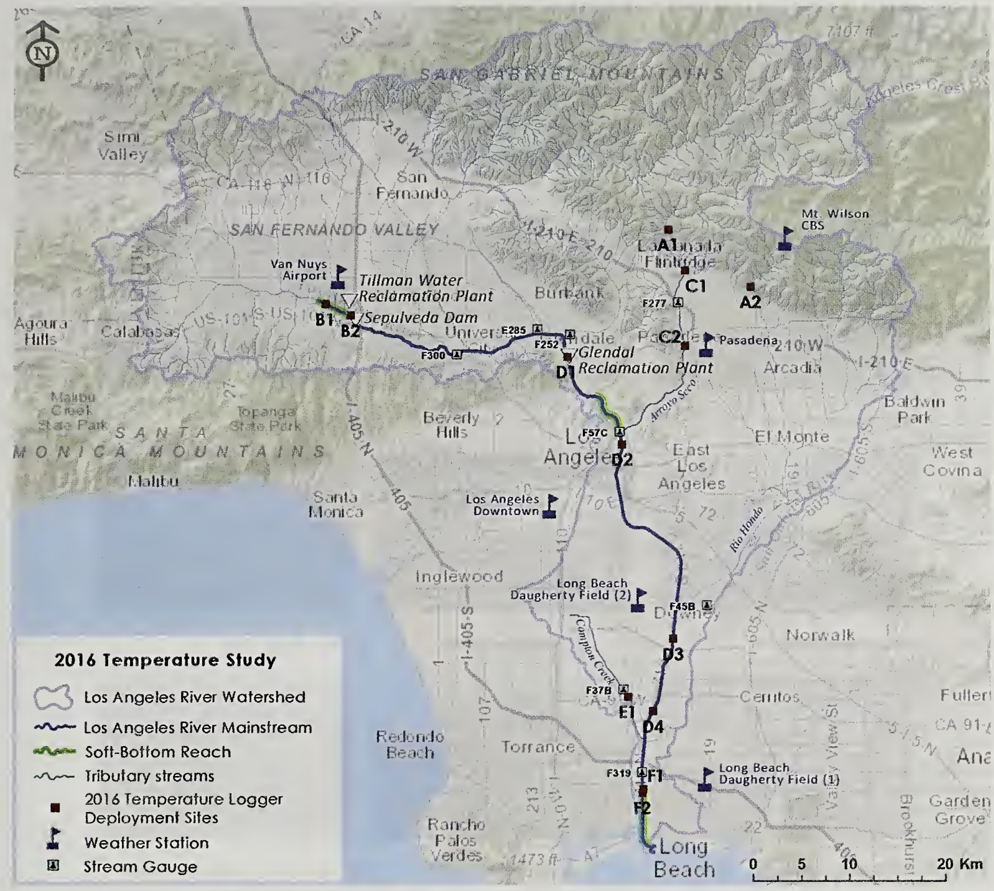


Fig. 1. Study Area showing zones and temperature logger locations.

a geographic region are ascribed their own zones and the main stem was further divided into natural (B) and channelized sections (D). Sites representative of depth and canopy cover were chosen within each zone and temperature loggers were installed at 13 locations in May 2016 (Fig. 2). Sites were selected based on the following criteria: accessibility, safety, location with respect to soft bottom reaches, depth, canopy cover, and tributary inputs, and distribution along the river (Table 1).

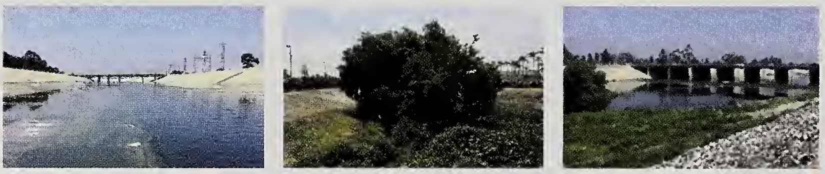
Water temperature data was collected from June through October 2016 using a combination of ONSET HOBO TidbiT v2 Water Temperature Data Loggers and HOBO Pendant Temperature Data Loggers (collectively, HOBOs) programmed to record time, date, and temperature. The TidbiT v2 has an accuracy of ±0.21°C and the Pendant has ±0.53°C accuracy; both are designed for use in outdoor and underwater environments. The study period was selected to align with southern California's dry season, with the highest air temperatures and lowest precipitation, when thermal stress on fish would be most likely to occur.

All loggers were prepared for deployment in the water column with appropriate site-specific materials to anchor them in place depending on site conditions (substrate, vegetation, access, etc.) and water depth. At all sites, the loggers were crimped to one end of an approximately one-meter long line of 90 lb-test stainless steel trolling wire using 1.40 mm leaden sleeves. The method used to anchor the other end of the wire to the stream channel varied depending on site

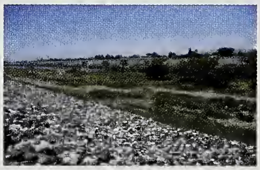
A1 Arroyo Seco A2 Eaton Wash B1 Balboa Bridge

B2 Burbank C1 Above Devil's Gate Dam C2 Rose Bowl

D1 Atwater Park D2 LA State Historic Park D3 Hollydale Park



D4 De Forest Park E1 Compton Creek F1 Willow St. Bridge (concrete)



F2 Willow St. Bridge (soft bottom)

Fig. 2. Photograph panel of Los Angeles River study sites June–October 2016.

conditions. For natural flow areas with mature vegetation, the devices were secured to a tree trunk, root, boulder or other stable object at the water's edge in such a way as to allow the logger to hang near the bottom of the water column while keeping it out of plain sight in order to reduce incidents of vandalism. For concrete channels and other areas where the previous method was not feasible, loggers were bolted to the channel wall. Weights were added to all wires to help prevent loggers from being swept up on shore during high flow events. Data loggers were not enclosed in protective housing, were of similar coloration to the surrounding substrate, and were only protected from direct sunlight where sufficient riparian vegetation was present to provide shading.

Locations in Zone A were managed by the Council for Watershed Health through their Los Angeles River Watershed-wide Monitoring Program. Both sites in Zone A had one HOBO in

Table 1. Site characteristics of the Los Angeles River water temperature monitoring locations.

Zone	Region	Site	Location	Channel type	Logger depth (in)	Distance from river mouth (mi)	Reach type	Data range
A	Angeles National Forest	1	Arroyo Seco	Soft Bottom	8	39.92	Tributary	Jun–Oct
		2	Eaton Wash	Soft Bottom	5	35.66	Tributary	Jun–Oct
B	Western San Fernando Valley	1	Balboa	Soft Bottom	30	45.9	Main Channel	Jun–Oct
		2	Burbank	Soft Bottom	20	44.4	Main Channel	Jun–Oct
C	Arroyo Seco	1	Above Devils Gate Dam	Soft Bottom	4	36.2	Tributary	Jun–Oct
		2	Rose Bowl	Soft Bottom	12	31.8	Tributary	Jun–Oct
D	Glendale Narrows	1	Atwater Park	Soft Bottom	24	30.5	Main Channel	Jun–Aug
	Downtown Los Angeles to Rio Hondo	2	L.A. State Historic Park	Concrete	24	24.4	Main Channel	Jun–Jul
		3	Hollydale Park	Concrete	24	12.1	Main Channel	Jun–Oct
	Compton to Dominguez Gap	4	DeForest Park	Concrete	24	8.0	Main Channel	Jun–Oct
E	Compton Creek	1	Compton Creek	Soft Bottom	20	8.8	Tributary	Jun–Sep
F	Long Beach Estuary	1	Willow St. Bridge	Concrete	20	3.7	Main Channel	Jun–Oct
		2	Willow St. Bridge	Soft Bottom	20	3.6	Main Channel	Jun–Oct

Table 2. Summary of potential and missing data points (148 days) at each site for the study period of June 4, 2016 at 12:00 to October 30, 2016 at 18:00.

	A1	A2	B1	B2	C1	C2	D1	D2	D3	D4	E1	F1	F2
Potential Data Points	886	886	7117	7117	7117	7117	7117	7117	7117	7117	7117	7117	7117
Missing Data Points	99	20	197	196	98	1	3515	5184	7	21	2140	1	57
Missing Data Days	12	4	4	4	2	0	73	108	0	0	45	0	1

the water recording temperature every four hours and one HOBO outside the water recording air temperature at the same four-hour interval. Data recorded at these sites were provided in a Microsoft Excel file for comparative analysis. Locations in Zones B-F had one HOBO per site recording water temperature at 30-minute intervals. Each site was visited monthly by trained citizen science volunteers to download the recorded data, ensure loggers were secure, and photograph site conditions. Data from each logger was offloaded using a HOBO U-DTW-1 Waterproof Shuttle Data Transporter in the field, which was subsequently uploaded to a computer using Hoboware PRO software, then compiled in a Microsoft Excel database.

Data points available at each site varied due to environmental factors affecting temperature readings (e.g. dry-downs, washouts, etc.), theft or vandalism, and equipment malfunction. These factors affected both the thermometer's ability to record data and its ability to take data representative of river conditions. Of all potential data points, less than 15 percent were absent for the entire study period across all sites. The majority of missing data occurred at sites D1, D2, and E1 (Table 2).

Water temperature data recorded from study reaches were summarized to establish a daily maximum, minimum, and mean temperature for each site. These daily metrics were combined to establish monthly mean, maxima, and minima. Temperature metrics were compared between study sites: 1) to examine differences between concrete and natural bottom locations; 2) to examine differences between sites in the main stem and tributaries; 3) to calculate the frequency, time of day and duration when temperatures exceed thermal limits for target native fish species; and 4) to map the changes in temperature throughout the river.

A quality assurance/quality control process to ensure data accuracy included several levels of review. The first level occurred when HOBO readings were imported into Microsoft EXCEL, and included completeness and examination for unusual outliers or missing information. Then, difference in temperature readings between consecutive data points was analyzed in an effort to differentiate between natural extreme changes in temperature, unnatural extreme changes in temperature representative of river conditions, and unnatural extreme changes in temperature that are not representative of river conditions (HOBO being handled or out of water during temperature recording). Table 2 summarizes the completeness of data collected between June and October 2016.

Precipitation and daily minimum and maximum air temperature records were obtained from five different NOAA weather stations throughout the Los Angeles basin. Daily flow data was obtained from Los Angeles County Department of Public Work's eight gauging stations in the Los Angeles basin. Weather stations and stream gauges are mapped in Fig. 1. The data obtained was examined for relationships with water temperature. Correlations between daily maximum water temperatures and daily maximum air temperatures and flow measurements were determined independently for each site. Daily maximum air temperatures showed a high degree of collinearity (not shown), so subsequent analyses utilized daily maximum air temperature from the Mount Wilson weather station. The sole exception was site C1, at which daily maximum water temperatures showed the highest correlation to air temperature data from the Long Beach weather station. Data from the flow and weather station with the highest correlation coefficient for each site was used in a multiple regression with daily maximum water temperature as the dependent variable. All analyses were performed in R[8].

Results

Between June and October 2016, the highest daily maximum water temperatures occurred in mainstem concrete bottom reaches (D2, D3, D4), while lower temperatures occurred in tributary reaches with more natural substrate and riparian vegetation (A1, A2, C1, C2, E1) (Fig. 3). Site D1, along the main stem with natural substrate and concrete banks, exhibited the highest daily maximum temperatures particularly in June and July. Less urbanized sites B1 and B2 in the Sepulveda Basin showed moderate daily maximum temperatures compared to other sites, while the estuary sites (F1 and F2) demonstrated more variability in maximum daily temperatures across the season than other sites, probably due to tidal influence. At site F2, overnight high temperatures are in close coordination with late night high tides.

The maximum water temperatures observed in all study sites are shown by month in Table 3. Monthly maximums were lowest in tributaries (Zones A, C, E). Highly urbanized main stem sites recorded the highest maximums (Zone D), and less urbanized main stem areas were mid-range (Zone B). Maximum temperatures showed the widest range in June, with readings ranging from 20.6°C to 36.8°C. Channelized sites D1 and D2 reached their highest temperatures in the month of June, while channelized sites D3 and D4 reached their highest temperatures in July. The highest single temperature reading of the season was recorded at the Long Beach Estuary site F1 in August. The other estuary site F2 also experienced its highest temperature during the month of August. Compton Creek E1 was the only site to record its highest maximum temperature in September.

Zone B sites had the most consistent monthly maximums. All other sites showed more variation in maximums from month to month. The most extreme monthly maximum variation occurred at site C1 with monthly maximums of 20.9°C, 22.1°C, 36.7°C, 25.4°C, 33.3°C occurring in June through October respectively. However, this was the shallowest site, and dry downs were a continuous issue, requiring relocation of the logger on multiple occasions throughout the study period. The highest temperatures recorded at C1, therefore, are most likely due to water receding to such extent that the logger recorded air temperature for some time before being relocated to a deeper pool.

Overall, monthly minimum water temperatures show less variation across sites than monthly maximums (Fig. 4). Sites B1 and B2 in Sepulveda Basin had the highest minimum temperatures, but also had the smallest monthly ranges (3.6–7.1°C) and recorded relatively cool maximums compared to other sites. In sites with concrete bottoms, the range between monthly maximum and minimum is greater (13.2–20.1°C). Zone A sites in the Angeles National Forest consistently had the lowest minimums throughout the season followed by site C1 (a fairly remote and natural tributary reach just downstream of A1). A short distance downstream, site C2 also recorded relatively low minimums during June and July. The lowest mean water temperatures were recorded in tributary sites A1, A2, C1, C2, and E1. Sites B1 and B2 in the less heavily urbanized Sepulveda Basin portion of the study area had the highest monthly averages and the smallest ranges of temperatures between monthly maximum and minimum.

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[8] R Core Team. 2016. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

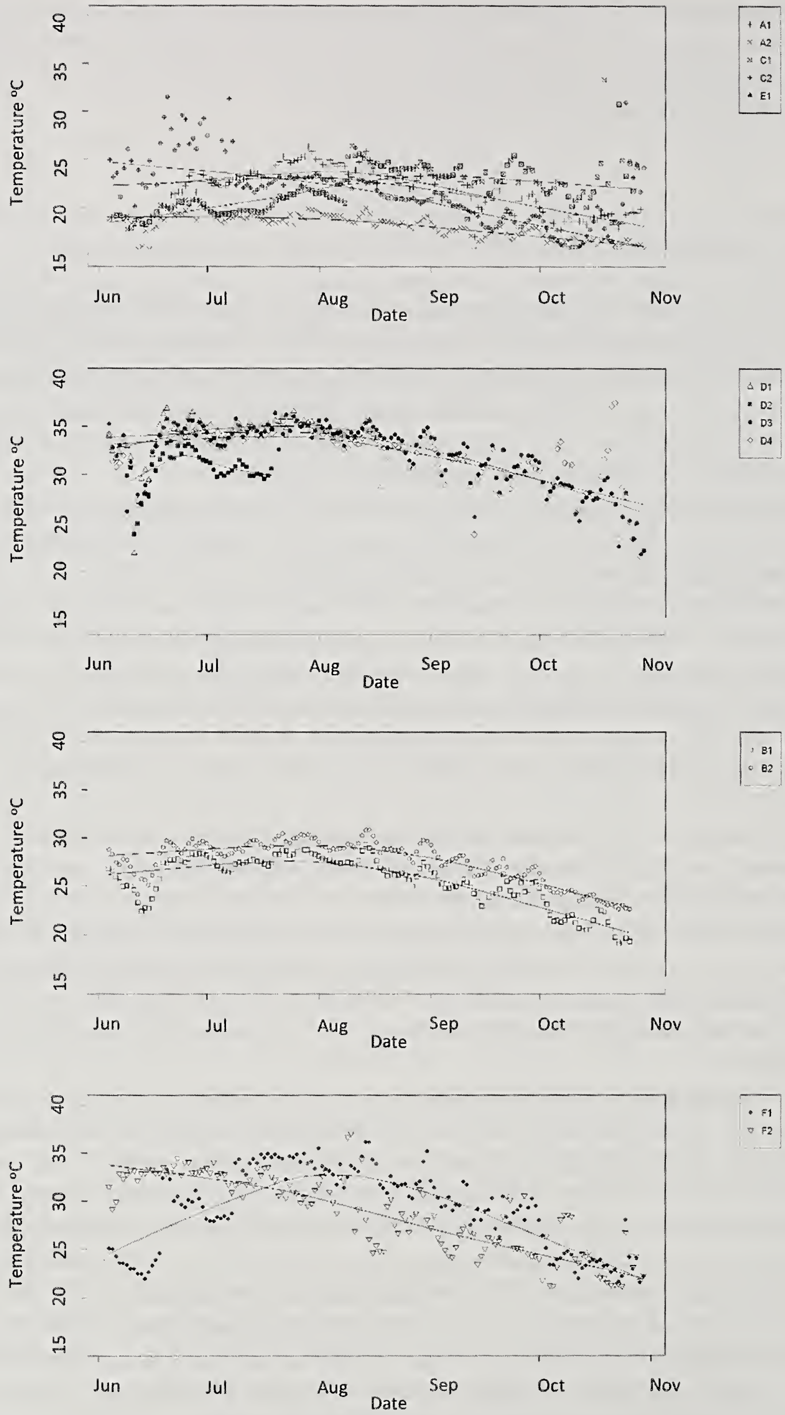

Fig. 3. Daily maximum temperatures at all sites plotted by date between June – October 2016. Smoothed lines are shown.

Table 3. Maximum water temperatures (max), minimum water temperatures (min), and range between maximum and minimum water temperatures each month (range). Highest maximum water temperatures for each month shown in bold; highest maximum water temperature for each site underlined.

	June			July			Aug.			Sept.			Oct.		
Site	Max	Min	Rng	Max	Min	Rng	Max	Min	Rng	Max	Min	Rng	Max	Min	Rng
A1*	23.7	17.2	6.5	26.3	16.7	9.6	25.8	15.8	10.0	23.5	13.7	9.8	19.9	13.8	6.1
A2*	20.6	13.7	7.0	19.9	14.0	5.8	19.9	13.8	6.1	18.5	13.8	4.8	17.7	13.5	4.2
B1*	28.4	21.2	7.1	28.7	25.1	3.6	29.3	23.8	5.5	26.7	21.7	5.0	24.8	18.4	6.3
B2*	29.9	22.8	7.0	30.5	25.9	4.6	30.8	25.5	5.4	29.3	23.3	6.0	26.3	19.9	6.4
C1*	20.9	15.2	5.7	22.1	17.8	4.4	36.7	16.0	20.7	25.4	14.4	11.0	33.3	13.4	20.0
C2*	31.5	14.4	17.1	31.3	17.8	13.5	26.2	19.7	6.5	21.6	17.2	4.4	31.0	15.1	15.9
D1*	**36.8**	17.1	19.7	**36.5**	19.8	16.8	35.5	19.1	16.5	-	-	-	-	-	-
D2	33.2	20.0	13.2	31.5	23.5	8.0	-	-	-	-	-	-	-	-	-
D3	35.7	17.2	18.6	36.4	20.6	15.7	35.6	19.8	15.8	**33.8**	17.4	16.4	31.3	17.0	14.3
D4	35.6	16.7	18.9	35.7	20.4	15.3	34.9	19.5	15.4	33.3	17.0	16.3	**33.4**	13.2	20.1
E1*	26.4	16.5	9.9	25.0	19.7	5.4	26.8	19.6	7.2	29.5	17.7	11.8	-	-	-
F1	33.3	20.9	12.4	34.9	20.3	14.6	36.1	19.6	16.5	32.1	17.5	14.6	28.0	17.5	10.5
F2*	34.4	21.3	13.1	34.0	20.2	13.8	**37.0**	18.6	18.4	30.6	17.5	13.1	28.6	15.4	13.1

* indicates natural bottom location

Hourly variation is shown in Fig. 5. Throughout the study period, the coolest temperatures in the LAR were recorded in the early morning, between 06:00 and 08:00, except for site F2 whose coolest hour on average was 11:00 (Table 4). The highest temperatures occurred between 13:00 and 20:00, with the majority of sites peaking between 14:00 and 16:00. Greater diurnal variation occurred in highly urbanized zones at D2, D3, E1, and F1, while diurnal variation was much diminished in more natural sites with soft bottoms and riparian vegetation such as sites A1, A2, C1, and C2. In the less urbanized Sepulveda Basin in the San Fernando Valley region, sites B1 and B2 were warmer overnight throughout the whole season. Average nighttime (17:00–05:00) temperatures were 0.53°C warmer than average daytime (05:00–17:00) temperatures at site B1 and 0.86° warmer at site B2. This pattern of warmer overnight temperatures was also observed at the estuary sites F1 and F2. Nighttime temperatures were 3.07°C warmer than daytime temperatures at F1, and 0.95°C warmer at nighttime than daytime at F2 throughout the study period.

The highest seasonal water temperatures occurred in the most heavily developed portions of the watershed, namely D1, D2, D3, and D4, all with average maximum temperatures for the season topping 30°C (Table 5). Site D1 had the highest temperatures of the season (average maximum $T = 34.1$°C). This site has a natural substrate bottom but concrete lined banks. This site also demonstrated the largest difference between average maximum and average minimum temperatures during the study period. The lowest temperatures in the watershed were recorded in Zone A, a relatively natural portion of the watershed found within the Angeles National Forest. The main stem channel reaches in the Sepulveda Basin (B1 and B2) showed the most stability with a 1.4° and 2.3° difference between seasonal average maximum and seasonal average minimum temperatures. Fig. 6 illustrates these temperatures in a longitudinal profile throughout the watershed to highlight thermal barriers to movement of native fishes from headwaters to the ocean and vice versa.

The changes in water temperature along the longitudinal continuum of the river from headwaters to estuary are illustrated in Fig. 7. The range of temperatures at each site are plotted

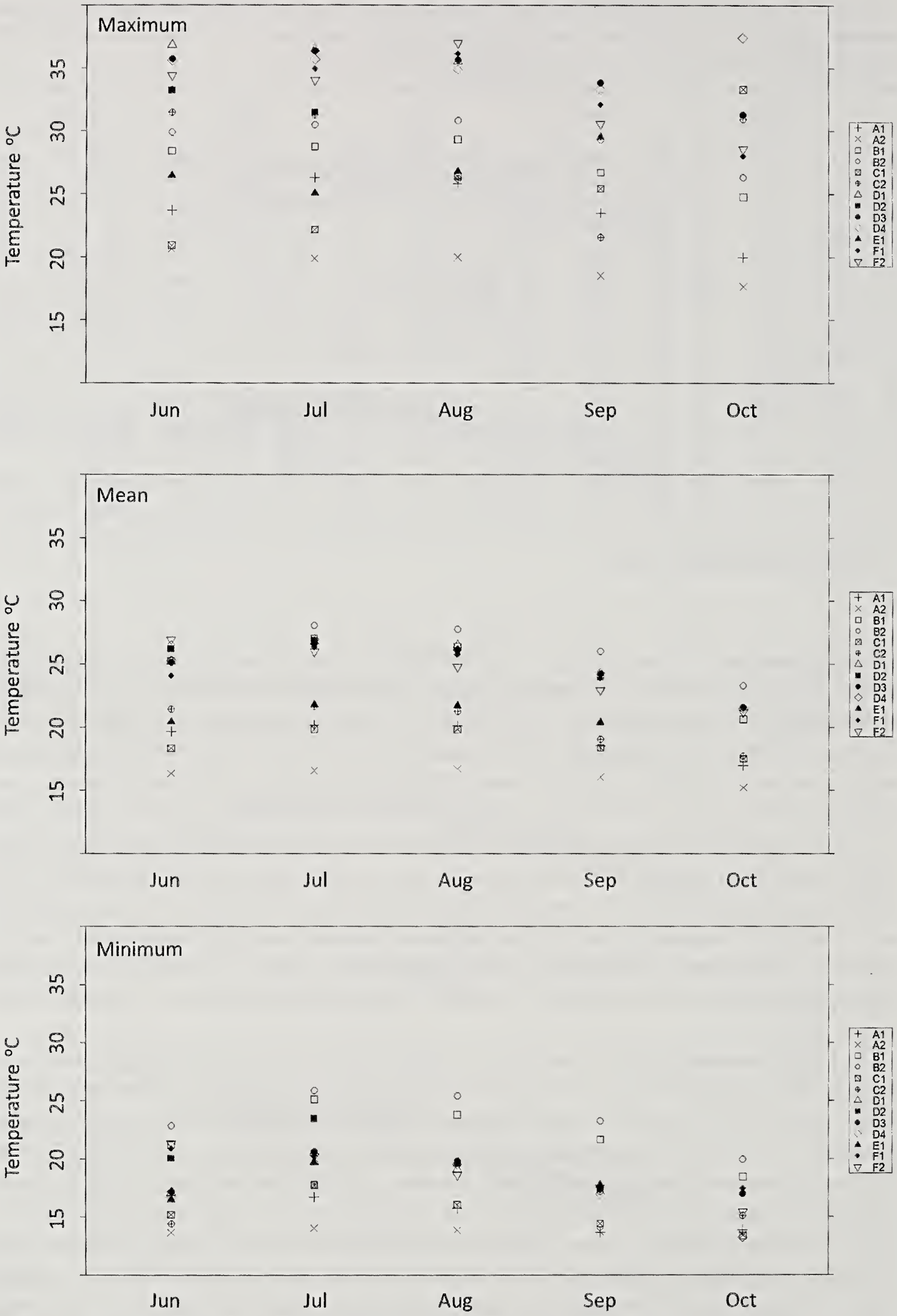

Fig. 4. Monthly maximum, mean, and minimum water temperatures taken at 13 sites in the Los Angeles River between June–October 2016.

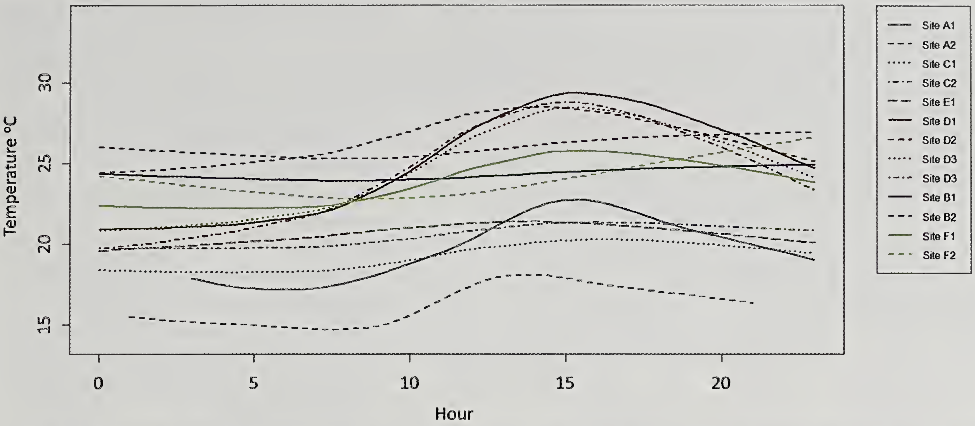

Fig. 5. Average hourly temperatures of 13 sites in the Los Angeles River between 4 June 2016 at 12:00 and 31 October 2016 at 18:00. Lines are smoothed over individual hourly points.

against the estimated temperature over which *O. mykiss* begin to show signs of behavioral stress (24°C). Although other target native fish species may be able to tolerate higher temperatures, 24°C was selected as the thermal limit because it would protect the majority of life stages of most native fish species. Apart from the headwaters that already support native fishes, most of the LAR surpasses this threshold, creating thermal barriers that could prevent movement from headwaters to the ocean and vice versa, access to refugia, and even year-round survival of native fish species.

Maximum daily water temperature from all sites, with the exception of C1, showed a significant positive correlation with maximum daily air temperature from the Mount Wilson weather station in the multiple regression (Table 6). Sites D2 and D3 showed the highest correlation coefficients, while sites C2 and F2 had the lowest. Maximum daily temperature from site C2 had a non-significant positive correlation with maximum daily air temperature from the Long Beach weather station. Five sites had a significant negative correlation with flow measured at Los

Table 4. Timing of maximum and minimum average hourly temperatures at sites in Los Angeles River June through October 2016.

	Max		Min	
Site	Time	°C	Time2	°C2
A1	13:00	18.00	9:00	14.93
A2	15:00	21.95	7:00	16.93
B1	19:00	25.43	8:00	24.19
B2	18:00	27.49	8:00	25.36
C1	14:00	21.36	7:00	17.37
C2	16:00	21.35	7:00	19.24
D1	15:00	33.93	7:00	20.77
D2	14:00	30.09	6:00	23.76
D3	16:00	31.28	7:00	20.65
D4	15:00	31.24	6:00	20.01
E1	15:00	22.24	6:00	20.44
F1	16:00	28.63	7:00	21.25
F2	20:00	26.59	11:00	23.00

Table 5. Seasonal average maximum, mean and minimum temperatures at each site from June 4, 2016 to October 30, 2016.

Site	Site name	Max	Mean	Min	Notes
A1	Arroyo Seco	21.9	19.1	16.9	Natural channel and banks; upper watershed tributary
A2	Eaton Wash	18.0	16.2	14.8	Natural channel and banks; upper watershed tributary
B1	Balboa	25.6	24.8	24.2	Deep and wide soft bottom reach with natural riparian vegetation on mainstem
B2	Burbank	27.6	26.4	25.3	Deep and wide soft bottom reach with natural riparian vegetation on mainstem
C1	Above Devils Gate Dam	22.0	18.8	17.3	Natural channel and banks; native riparian vegetation; shallow tributary upstream of Devil's Gate Dam.
C2	Rose Bowl	21.8	20.2	19.0	Soft Bottom with riparian vegetation; tributary in urbanized area downstream of Devil's Gate Dam and the Rose Bowl.
D1	Atwater Park	34.1	26.2	20.7	Soft bottom. Just upstream of Glendale Water Reclamation Plant. Some riparian and in-channel vegetation.
D2	L.A. State Historic Park	30.5	26.5	23.7	Concrete channel in heavily urbanized area. No vegetation.
D3	Hollydale Park	31.9	24.8	20.5	Concrete channel in heavily urbanized area. No vegetation.
D4	DeForest Park	31.6	24.8	19.9	Concrete channel in heavily urbanized area. No vegetation.
E1	Compton Creek	22.8	21.2	20.2	Soft bottom, tributary reach in urbanized area with riparian vegetation.
F1	Willow St. Bridge	29.2	24.4	21.1	At end of concrete channel entering estuary.
F2	Willow St. Bridge	28.7	24.3	21.1	Soft bottom estuary.

Angeles County Burbank-Western Storm Drain station E285F. Site E1 had a positive correlation with flow data, but this value was not statistically significant.

Discussion

In streams like the Los Angeles River that are maintained for flood control, channelization can be a strong driver of the thermal regime. Simplifying the physical structure of the river channel eliminates natural thermal buffers and insulators (Poole and Berman 2001), causing water temperature to be vulnerable to fluctuations in ambient air temperature and solar radiation. Confining a stream to a concrete channel also eliminates the stream's connection with groundwater, resulting in loss of the natural buffering effect that groundwater has on stream temperatures. In addition, concrete lining on the streambanks absorbs solar energy and radiates heat due to the thermal mass of the construction materials (Hester and Doyle 2011).

Land use activities that increase impervious surfaces outside the stream channel also alter the amount of water flowing into the stream and its timing and temperature (Poole et al. 2001a; 2001b). High temperature pulses can occur in urban streams because runoff from impervious surfaces can result in highly variable temperatures over short time scales (Van Buren et al. 2000). During the winter months, stormwater runoff accounts for the majority of the water flowing through the concrete channels designed for flood control, but flow into the LAR during our study period from June to October was mostly comprised of non-point source "urban drool"

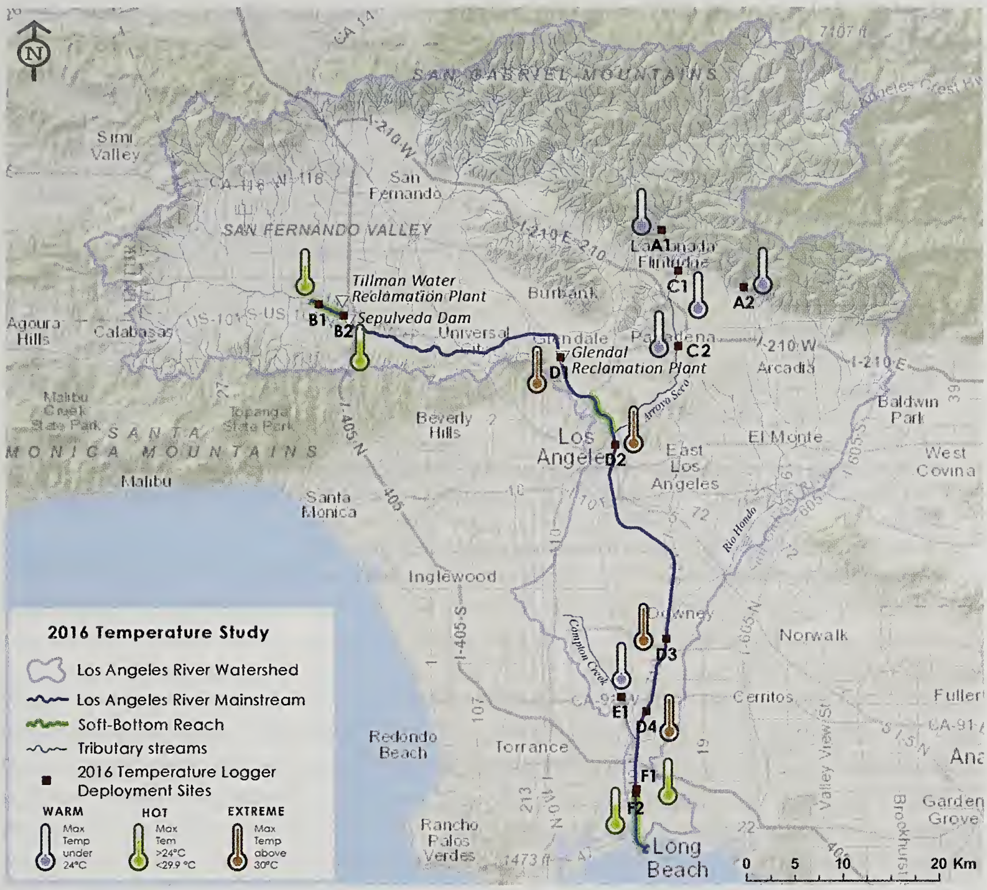

Fig. 6. Los Angeles River seasonal average maximum temperatures from estuary to headwaters.

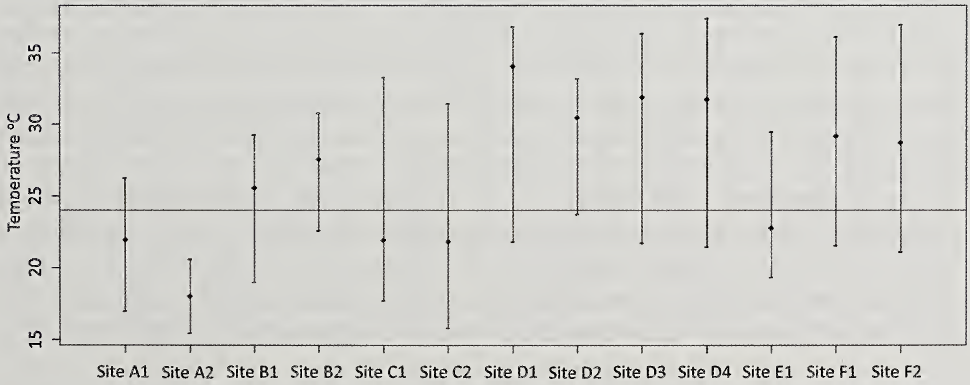

Fig. 7. Temperature ranges for sites in the Los Angeles River June–October with thermal limit of 24°C for target native fish species.

Table 6. Correlation coefficients between maximum daily water temperature and maximum daily air temperature/flow in the Los Angeles River. All air temperature data was from the Mount Wilson weather station unless indicated. Multiple R^2 from the multiple regression is also reported.

Site	Max. air temp.	Flow[a]	Multiple R^2
B1	$r = 0.646^{***}$	$r = -0.202$; F252	0.417
B2	$r = 0.676^{***}$	$r = -0.208$; F252	0.457
C1	$r = 0.220$[b]	$r = -0.434^{***}$; E285	0.199
C2	$r = 0.350^{***}$	$r = 0.350^{***}$; E285	0.305
D1	$r = 0.633^{***}$	$r = -0.558^{**}$; F252	0.532
D2	$r = 0.751^{***}$	$r = 0.436^{***}$; F300	0.588
D3	$r = 0.738^{***}$	$r = -0.299^{**}$; E285	0.569
D4	$r = 0.734^{***}$	$r = -0.304^{**}$; E285	0.565
E1	$r = 0.448^{***}$	$r = 0.243$; F319	0.231
F1	$r = 0.614^{***}$	$r = -0.482^{***}$; E285	0.512
F2	$r = 0.430^{***}$	$r = -0.218$; F319	0.199

[a] Flow data from the station used in the multiple regression is reported after the correlation coefficient.
[b] Daily maximum air temperature data from the Long Beach weather station.
** Indicates variable was significant in the multiple regression with $p < 0.01$
*** Indicates variable was significant in the multiple regression with $p < 0.001$

surface runoff, runoff from very minor rain events (less than 1-inch total in most areas over the watershed during the study period), and releases from water treatment facilities. Releases from water reclamation plants account for the majority of the LAR's base flow and could play a key role in regulating water temperatures. The Donald C. Tillman Water Reclamation Plant, a leading producer of reclaimed water in the San Fernando Valley, releases approximately 80 million gallons of tertiary treated water per day into the LAR basin. Treated water is distributed to three nearby lakes (the Japanese Garden Lake, the Wildlife Lake, and the Balboa Recreation Lake) and directly into the LAR just above site D1. The Los Angeles/Glendale Water Reclamation Plant processes an additional approximately 20 million gallons a day to tertiary standards, and releases water to the LAR just downstream of D1[9].

By comparing different sites within the same system that are subject to varying conditions of concrete channelization, urbanization, riparian cover, and flow augmentation, we began a rudimentary isolation of specific effects on maximum, minimum, and mean water temperatures, and their influxes and ranges longitudinally through the watershed. We found that the smallest range of water temperatures occurred in the upper watershed in the Sepulveda Basin of the western San Fernando Valley, where the channel has a soft bottom, significant depth and width, and extensive riparian vegetation lining the banks and overhanging the wetted channel. While the natural conditions of this reach seem to moderate water temperatures from extreme fluctuations, the overall temperatures of the two sites (B1, B2) remained high. Water temperatures in July never dropped below 24°C, which is often considered the lower limit of the critical thermal maxima for *O. mykiss* (Boughton and Palmer 2007; Boughton et al. 2015; Myrick and Cech 2000; Myrick and Cech 2005; Spina 2007; Sloat and Osterback 2012; Table 7). Throughout the entire study period, only 36% of days at site B1 and 27% of days at site B2 did not exceed 25°C.

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[9] LA City Department of Sanitation. 2017. Los Angeles-Glendale water reclamation plant. Available from www.lacitysan.org/, Accessed 1 May 2017.

Table 7. Reported thermal limits for target native fish species.

Scientific name	Common name	Max. temp.	Source
Catastomus santanae	Santa Ana sucker	22°C, 26.7°C – 32.8°C	Moyle 2002, USFWS 2014
Gasterosteus aculeatus williamsoni	unarmored threespine stickleback	30.4°C – 34.6°C	Feldmeth and Baskin 1976
Oncorhynchus mykiss	rainbow / southern steelhead trout	23°C – 31.5°C	Bell 1986, Boughton et al. 2007, Boughton et al. 2015, Myrick and Cech 2000, Myrick and Cech 2005, Spina 2007, Sloat and Osterback 2012
Gila orcutti	Arroyo chub	28°C	O'Brien 2009, Moyle et al. 2015
Rhinichthys osculus ssp.	Santa Ana speckled dace	20°C	Moyle et al. 1995

Downstream in the main stem of the river near D1, the water temperature range expanded, with differences in monthly maximum and minimum temperatures ranging from 16.5 to 19.7°C. The natural bottom site is located downstream of a long stretch of simplified concrete channel surrounded by multi-lane State Highway Route 5 and miles of impervious surfaces that are devoid of thermal buffers and insulators, save a small amount of heavily managed in-channel and riparian vegetation. The concrete bank itself radiates absorbed solar energy as well (Van Buren et al., 2000). The monthly minimums and maximums at D1 were all more extreme than those observed in Zone B (B1, B2). D1 recorded monthly maximums in the mid-30s in June, July and August, and monthly minimums in the teens, whereas in Zone B monthly maximums did not exceed 30.8°C and minimums did not drop below 21°C in the same months.

Water from tributary reaches in Zones A (A1, A2) and C (C1, C2) enters the mainstem of the LAR between sites D1 and D2. Water temperatures at all sites in Zones A and C were lower than those in the mainstem. The two sites in the Angeles National Forest (A1, A2) had the lowest temperatures overall, while the two Arroyo Seco tributary sites (C1, C2) also remained cooler than the main stem locations, although warmer than the sites in Zone A. As expected, water temperatures increased as the tributary neared the urban center, and the influence of impervious surfaces and urban runoff increased. Intact riparian vegetation and substantial canopy cover at site C2 is likely responsible for helping to moderate temperatures despite being surrounded by urban development, although that effect was not evident in the Sepulveda Basin sites (B1 and B2) where despite well developed riparian bank cover, temperatures remained high with little variation in range from maximum to minimum. Lower temperatures at site D2 as compared with D1 indicate that an inflow of cooler water from the Arroyo Seco tributary may impact water temperature at that location, although there is not yet sufficient data to confirm this hypothesis.

Theft or loss of thermometers in the highly visible concrete channels resulted in limited data sets for a large geographic area along the central main stem of the river. Despite the limited data, trends appear to be consistent in the main channel between sites D1 and D4. The highest daily and monthly maximum water temperatures consistently occurred in Zone D. Zone D also experienced greater diurnal variation. The water temperatures in this zone showed a strong correlation to air temperatures, indicating that, lacking vegetation, substrate, and groundwater influence, the water temperatures in these concrete channels are easily influenced by fluctuations in air temperature.

The 13.6 km-long Compton Creek is a highly urbanized subwatershed that enters the LAR channel between sites D4 and F1. The upper 9.3 km of this tributary is contained within a concrete box channel, while the remaining lower 4.3 km has a soft bottom, native riparian vegetation, and concrete sides. Site E1 is located within this lower soft-bottom reach of the tributary. Although heavily influenced by impervious surfaces and urban runoff, E1 demonstrated lower temperatures than those of the mainstem sites, further emphasizing the important role of intact riparian vegetation, canopy cover, and groundwater interactions on stream temperature.

Nearing the river mouth, the sites at the Long Beach Estuary (F1, F2) showed unusual trends. Despite being placed 0.16 km apart and having the widest channels in the study area with potentially more thermal holding capacity, the influence of the concrete channel closer to site F1 compared to the more tidally influenced site F2 resulted in water temperature peaks at much different times. Maximum average hourly temperatures at site F1 occurred at 16:00 and minimum average hourly temperatures occurred at 07:00, which is consistent with the hourly fluctuations of sites further upstream. At F2, however, maximum average hourly temperatures peaked at 20:00 and minimum average hourly temperatures occurred at 11:00 suggesting that tidal fluctuations could also have played a role in the timing differences in temperature extremes. At site F2, late night high tides were in close coordination with overnight temperature peaks, which was not the case at site F1, a shallower site with less salt water or stratification.

Conclusions

Using the estimated thermal limit of 24°C, water temperatures throughout the mainstem of the Los Angeles River would be exceedingly challenging for key native fish species such as rainbow/steelhead trout, arroyo chub, Santa Ana sucker, and Santa Ana speckled dace (Table 7). Although the water temperatures are cooler during the winter migratory season, the current temperature regime creates thermal barriers for fish movement through the watershed during the warmer summer season and isolates current populations of native fish to the tributaries in the Angeles National Forest where temperature only exceeded 24°C for 19% of days in the study period at A1, but never at A2. While currently the extreme temperatures do support a wide range of non-native generalist fish species in the mainstem, summer season temperature mitigation is imperative for the reintroduction of native fishes. Even though some native fish species are able to survive temperatures close to 30°C, they all require cooler temperatures for successful reproduction and juvenile rearing.

Comparison of channelized to non-channelized reaches suggests that channelization widens the temperature range (higher maximum, lower minimum). The most natural tributaries in the Angeles National Forest recorded the lowest temperatures overall. However, channels with natural substrate and riparian vegetation exhibited temperatures in the mid-range as they entered increasingly urban areas having more impervious surfaces near the stream channel. Mainstem sites with concrete banks and bottoms as well as site D1, with concrete banks and a soft bottom experienced the most temperature fluctuation. Lack of shade that would be provided by overhanging vegetation on natural banks; lack of connection with groundwater to moderate the temperature of surface flow; and the capacity of concrete structures to absorb and re-radiate solar energy all contribute to an increased temperature range. The role of continuous input of tertiary treated waters into the LAR should be further examined. Since the temperature of released wastewater effluent is consistent year-round, it is conceivable that the warming effect caused by released effluent in the cool winter months may have the reverse effect in the warmest part of the year, actually cooling instream temperatures and providing refugia for aquatic species.

Although this paper is limited in scope, our study points to both channelization in the mainstem and the heat island effect created by surrounding urbanization as major sources of thermal stress in the Los Angeles River watershed. However, further studies with more loggers over a longer period would be necessary to isolate heat sources and understand their synergistic effects. Use of more sophisticated monitoring technologies, such as fiber optic sensors and thermal infrared remote sensing, would further the scientific understanding of the thermal regime of the river. Additionally, it is important to remember that reach scale restoration can work to de-channelize sites, but the restored stream may still be degraded (Purcell et al. 2002) due to other stressors such as dissolved oxygen. Further investigation of dissolved oxygen levels related to temperature and flow patterns throughout the river are needed as well. If reach scale restoration is to be successful it must be implemented as part of a larger strategy that works to mitigate the effects of underlying stressors (Bernhardt and Palmer 2007) that degrade the physical and chemical composition of instream water. While this pilot study provides a useful broad-brush overview of current conditions, expanding this effort is necessary in order to develop sufficient information to direct and guide restoration planning.

Acknowledgements

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Distribution of the Eastern Fox Squirrel (*Sciurus niger*) within California as of 2015

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Abstract.—The eastern fox squirrel, *Sciurus niger*, has been introduced to many areas outside of its native range. Once introduced to a new region the species has generally expanded its geographic range and is considered to be an invasive species, causing both ecological and economic harm. While some information is available on where introductions have occurred, detailed information is not available on the current geographic distribution of the species within California. Since invasive species tend to be under-represented in specimen collections at museums, new methods for obtaining location data were needed. We used a time period of 1995 through 2015 for observations so that location data would be most up-to-date. A majority (51%) of location data used in this study came from wildlife rehabilitation centers, approximately 31% came from citizen-science type sources such as the California Road-Kill Observation System, a previously published journal article, and research-grade submissions to iNaturalist, 10% came from the California Department of Public Health West Nile Virus Surveillance Program, and 8% came from the authors and trained student observers. Maps are presented to show the current geographic distribution of the species indicating a broader range than what was previously known.

The eastern fox squirrel, *Sciurus niger*- hereafter EFS, is native to the eastern and central United States and the southern prairie provinces of Canada, south of approximately 48°N latitude (Koprowski 1994) where they are known to live in forests, woodlands, agricultural landscapes and urban areas (Kleiman et al. 2004). In the native range, the EFS is most often found in deciduous and mixed forests and ideal habitats are small stands of large trees separated by agricultural land (Allen 1982). Ten subspecies of EFS are recognized based on size, coat color, and geographic location (Wilson and Reeder 2005). While four subspecies of the EFS are listed as threatened or endangered: *S. n. avicennia, S. n. cinereus, S. n. niger,* and *S. n. shermani* (Loeb and Moncrief 1993), it is thought that the subspecies present within California is *S. n. rufiventer* (Moncrief et al. 2010; Claytor et al. 2015). *Sciurus niger rufiventer* is the most wide-ranging subspecies within the native range of the species (Koprowski 1994; Wilson and Reeder 2005) and is characterized by a brown with buff or orange coloration on the back and sides, the abdomen being orange, cinnamon, or white in color (Koprowski 1994). It has been noted (AEM) that most EFS individuals observed within California have a cinnamon or orange colored abdomen but some individuals found around Sacramento and Davis have white fur on the abdomen.

Eastern fox squirrels have been intentionally introduced from portions of their native range of the mid-western United States to many urban and suburban areas within the western United

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States including areas within Arizona (Brady et al 2017), California, Idaho, Montana, Oregon, and Washington (Koprowski 1994). The species has reached the state of Colorado through natural range expansion (Geluso 2004; Hoover and Yeager 1953) and New Mexico through introductions (Frey and Campbell 1997). The species has also been observed in Laramie, Wyoming (AEM personal observation).

The first successful introduction of the EFS into California probably occurred to Golden Gate Park in San Francisco before 1890, although specific details related to this introduction are not known (Byrne 1979). The species was introduced to the city of Fresno from Missouri in 1900 or 1901 (Storer Papers). The first specimen recorded on the campus of Stanford University in Palo Alto, CA, which is 56 km south of Golden Gate Park in San Francisco, was in 1921 (Byrne 1979). Animals were also moved from Golden Gate Park in San Francisco to Sacramento in 1921 (Byrne 1979; Storer Papers) and animals appeared on the campus of the University of California, Berkeley circa 1926 (Boulware 1941). Animals, most likely from the east bay area of San Francisco, were moved to Mount Diablo in Clayton in 1960 (King 2004). The EFS was introduced to the Veteran's Hospital in Yountville within the Napa Valley at some early date, since they had spread significantly before the 1970s, and to Vacaville, which lies between San Francisco and Sacramento, as early as the 1930s (Byrne 1979).

Individuals from Fresno were used to establish a population at Mieke's Grove Park, located between Lodi and Stockton (Byrne 1979), making Fresno the most likely source of the current population around Stockton. Animals currently located in Merced may have come from Fresno as the species is not found in the City of Modesto, which lies between Merced and Stockton.

Eastern fox squirrels were released or escaped from captivity at the Veteran's Hospital in West Los Angeles in 1904. The source for this population was suggested as some region of the Mississippi Valley (Becker and Kimball 1947). Individuals also escaped from captivity at the San Diego Zoo in 1920 (Staff Writer 1929), establishing the current population within that city. The EFS was first observed in Santa Barbara in 2006 (personal records of Paul Collins, Curator of Vertebrates, Santa Barbara Museum of Natural History). Although the source population for Santa Barbara is not known, the EFS was found in Ventura 50 km to the southeast by the late 1960s (Wolf and Roest 1971). Animals were moved from Fresno to Bakersfield in 1985 (King 2004) and the EFS appeared in Kernville, which is located 84 km northeast of Bakersfield and adjacent to the Sequoia National Forest, from an unknown location prior to the late 1970s (S. Anderson, pers. comm.). An isolated population of the EFS has been present in the Wood Streets area of the City of Riverside, CA for at least the last 40 years (G. Garcia, pers. comm.). Information regarding the source of this population is unavailable.

With the exception of the introductions to Bakersfield, Sacramento, Stockton, and to Los Angeles, very little is known regarding the source populations of the founding animals, the number of founding animals to any specific area within California, or the number of separate introductions to any area over time. Molecular genetic techniques such as analysis of mitochondrial haplotypes could help sort out more details regarding transfers of animals within the state, and possibly source populations from outside the state. What is known is that the species has greatly expanded its range within California over the past ~125 years (Byrne 1979; King et al. 2010). This paper documents the range occupied by the EFS within California as of 2015 and provides some estimates of range expansion for the species with California.

In California, animals have dispersed from original points of introduction through natural dispersal and through intentional movement of animals by humans. For example, since the original introduction to Los Angeles, the EFS has expanded its range at rates up to 3.44 km/yr (King et al. 2010) although rates of about 1.50 km/yr may be more realistic within suburbanized habitats (Garcia and Muchlinski 2017). King (2004) reported many cases of intentional relocation of EFSs by residents of Los Angeles County where squirrels are often considered pests. Squirrels are often live trapped and released into parks and golf courses where the species was not present, thereby facilitating range expansion beyond what would occur through natural dispersal. The EFS has been hypothesized to compete with native western gray squirrels (*Sciurus griseus* – hereafter WGS) for resources such as nesting sites, space, and food, and the EFS has actively replaced the WGS within certain habitats in southern California (Muchlinski et al. 2009; Cooper and Muchlinski 2015). The EFS is considered a game species by the California Department of Fish and Wildlife with open seasons for hunting in parts of the state by use of gun, bow and arrow, or falcon. The Department of Fish and Wildlife also allows, but regulates, the intake and release of juvenile or injured EFSs by rehabilitation facilities throughout the state.

Materials and Methods

Location data from California were gathered over the time frame of January 1995 through August of 2015. Since specimens of invasive species such as the EFS in museum collections are very limited, other sources of location data were needed for this study. Of the 7,307 observations mapped for this study (Table 1), most location data (51%) were obtained from wildlife rehabilitation centers situated throughout the state of California. Some rehabilitation centers were able to provide detailed intake records from 1995 through 2014 while other centers could only provide records for 2014 and a few previous years.

Additional sources of data included the California Department of Public Health West Nile Virus Surveillance Program, the California Roadkill Observation System operated through the University of California - Davis, the Global Biodiversity Information Facility (GBIF) – searched on October 25, 2015 for museum specimens and iNaturalist Research Grade Human Observations from January 1995 through August 2015, a thesis produced by King (2004), information obtained through personal observations (AEM and graduate research students) and information obtained via a web-based survey form. Observations through iNaturalist are utilized here under a Creative Commons Non-Commercial License. Name attribution to contributors of information can be obtained through a search on GBIF[1].

Mapping results are presented at different landscape levels including the entire state of California and various regions of the state. Location addresses were converted to geographic coordinates by finding the latitude and longitude coordinates of each individual sighting through Google Maps. The coordinates were saved as a text file along with corresponding information related to species type, year observed, specific date seen if given, and additional information if given. The location information was added to ArcMap 10.2.2 for display purposes and projected to 1984 California State Plane (Albers).

Results

A state-level view of the current distribution of the EFS within California is shown in Fig. 1. From this landscape level, as well as in more detailed landscape levels, the vast majority of observations are located in urban and suburban areas of the state. This result is not surprising as (1) the original introductions took place in what are now highly urbanized/suburbanized areas, and (2) observations would tend to occur most frequently in areas inhabited by large numbers

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[1] https://www.researchgate.net/publication/313241828_Location_data_for_eastern_fox_squirrel_Sciurus_niger_within_California_from_1995-2015

Table 1. Sources of observations of the Eastern Fox Squirrel, *Sciurus niger*, from 1995 through 2015 within California.

Data source	Area	Location points
Alan Muchlinski and Students[1]	Statewide	329
California Department of Public Health[2]	Statewide	722
California Roadkill Observation System[3]	Statewide	703
Emails (Web Survey)[1]	Statewide	255
Julie King Thesis[1]	Los Angeles Area	757
Wildlife Rehabilitation Centers[4]		3714
California Living Museum	Bakersfield, CA	6
California Wildlife Center	Los Angeles Area	136
Critter Creek Wildlife Station	Fresno, CA	51
Gold Country Wildlife Rescue	Auburn, CA	29
Lindsey Wildlife Museum	Walnut Creek, CA	1995
Peninsula Humane Society	Burlingame, CA	15
SPCA Monterey County	Monterey County	88
Sonoma County Wildlife Rescue	Petaluma, CA	40
Squirrelmender Wildlife Rehabilitation	Ventura County	34
Stanislaus Wildlife Rehabilitation Center	Hughson, CA	11
Suisun Wildlife Rescue Center	Suisun, CA	127
Sulphur Creek Nature Center	Hayward, CA	361
Wetlands & Wildlife Care Center	Orange County	172
WildCare	San Rafael, CA	301
Wildlife Center Silicon Valley	San Jose, CA	348
Online Geodatabases		548
Global Biodiversity Information Facility[5]	Statewide	548
Grand Total		7307

[1] Location information and species identification from these sources were by observations of live animals in the natural environment.

[2] Location information was through coordinates of latitude and longitude, and species identification was by in-hand observation of deceased animals sent to the California Department of Public Health.

[3] Location information was through coordinates of latitude and longitude, and species identification was through observations of photographs.

[4] Location information was gathered from intake forms and species identification was by trained individuals who worked at the rehabilitation center.

[5] Location information and species identification from this source was through data from museum specimens or through observations, with photographs, by individuals using iNaturalist.

of people. However, it will be pointed out later in this section that the EFS is also found in areas with much lower human population density, ranging from rural to unpopulated areas.

Eastern fox squirrels introduced to Golden Gate Park in San Francisco have undergone significant range expansion to the south (Fig. 2). The species is currently found in an uninterrupted distribution to the south of San Francisco along the western side of San Francisco Bay, through San Jose and further south to the Cities of Gilroy, and Salinas, within the Santa Cruz Mountains, and in the City of Santa Cruz. A population of EFSs exists within the Cities of Monterey, Pacific Grove, and Carmel. Range expansion of the EFS also occurred from south to north along the southeastern portion of San Francisco Bay where animals met conspecifics undergoing range expansion from Berkeley south through Oakland, San Leandro, Hayward, and Freemont. The EFS has a continuous distribution along the eastern side of San Francisco Bay.

The EFS was first cataloged at WildCare Rehabilitation Center in the City of San Rafael, Marin County, CA, which lies north of the Golden Gate Bridge, in 2002 (Fig. 3). Possible

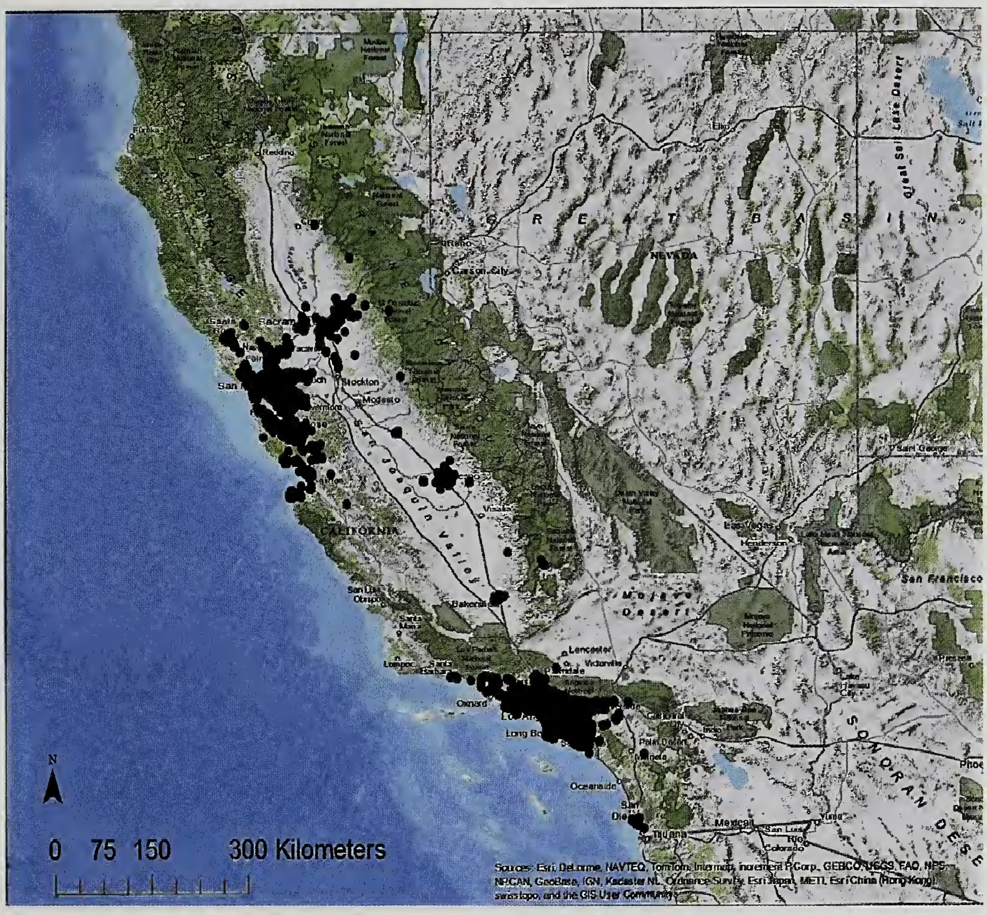

Fig. 1. Observations of the Eastern Fox Squirrel, *Sciurus niger*, in California over the time period 1995 through 2015. Maps throughout this paper were created using ArcGIS® software by Esri. ArcGIS® and ArcMap™ are the intellectual property of Esri and are used herein under license. Copyright © Esri. All rights reserved.

scenarios by which the species appeared in San Rafael could involve movement through human activity north of the Golden Gate Bridge into Marin County or movement south from the City of Santa Rosa where the species was found in the 1970s. Because the vast majority of collected observations are on the more southern end of the corridor, in Marin County, we believe it is most likely that the EFS was transferred across the Golden Gate Bridge sometime prior to the year 2000. The species now exists northward through San Rafael, San Anselmo, and Fairfax, north along the Highway 101 corridor through Petaluma, Rohnert Park, and Santa Rosa, and west to Sebastolpol. The species is also present within the full range of the Napa Valley from Napa northward to Calistoga.

In 1979, the population of the EFS around the east bay area of San Francisco and the population around Sacramento were separate populations; although the population in Sacramento had been founded by animals from San Francisco. By 2015 the two populations seem to have merged, or are very close to merging, forming one metapopulation from near Monterey north through the San Francisco Bay Area, then east through Davis and Sacramento to cities such as Auburn, Coloma and Grass Valley in the foothills of the Sierra Nevada Mountains (Fig. 3).

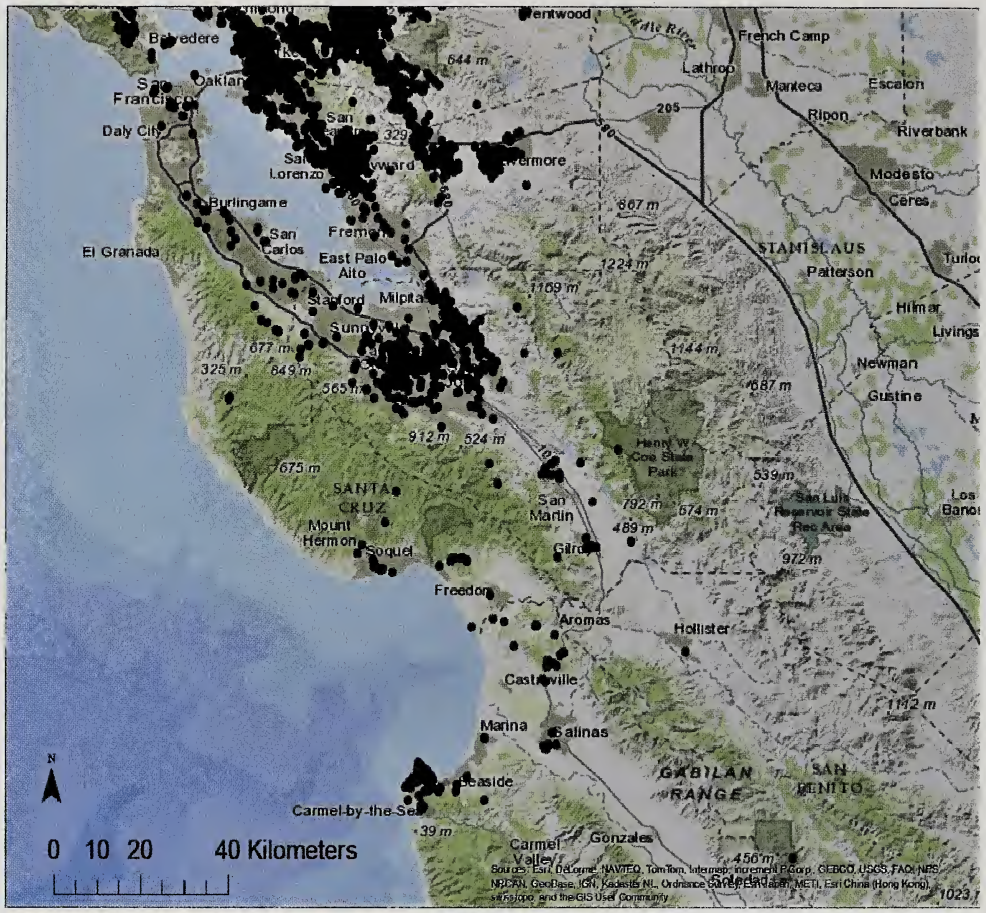

Fig. 2. Observations of the Eastern Fox Squirrel, *Sciurus niger*, in the area of the San Francisco Bay south to Monterey/Carmel and San Benito over the time period 1995 through 2015.

The distribution of the EFS around Fresno is not as closely linked to the urban/suburban areas of the city at it is in other parts of the state (Fig. 4). The agricultural area surrounding Fresno is rich in orchards of almond, peach, nectarine, and cherry trees. The EFS is found in almond orchards at least 30 km west of Fresno, including orchards west of the small town of Kerman, and it is also found 30 km east of Fresno along branches of the King River. Fruit orchards are fairly contiguous east of Fresno and Clovis to the foothills of the Sierra Nevada Mountain Range.

Following introduction to Los Angeles in 1904, range expansion has occurred in all directions so that the species is now found not only in Los Angeles County but also in Orange, Riverside, San Bernardino, Santa Barbara, and Ventura Counties (Fig. 5). It is unknown when range expansion to Santa Barbara County occurred but the species is now common throughout urban and suburban areas around Santa Barbara and Montecito; indicating rapid range expansion in the last couple of decades. Range expansion by the EFS has come at the expense of populations of native western gray squirrels at locations such as Ganna Walska Lotusland in Montecito and Rocky Nook Park in Santa Barbara (AEM personal observations). There appears to be a break between the population in the area around Santa Barbara and the population in the area around

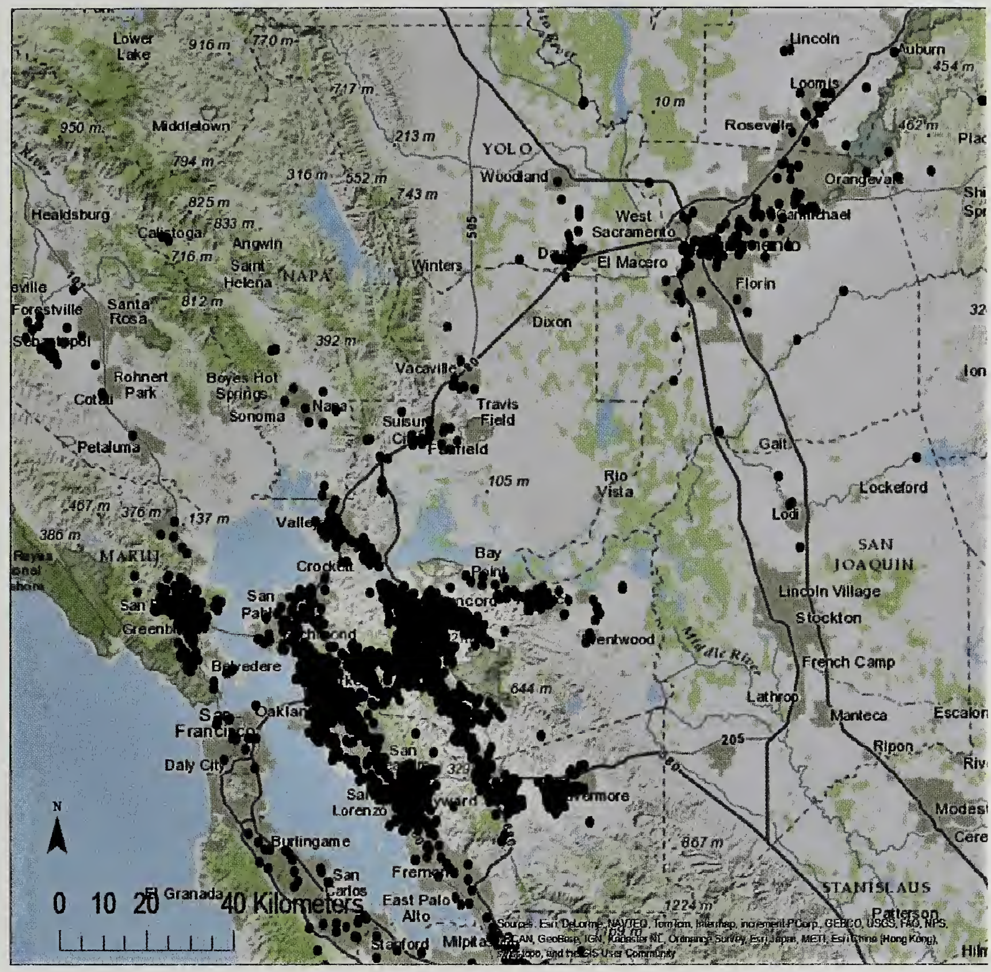

Fig. 3. Observations of the Eastern Fox Squirrel, *Sciurus niger*, to the north and east of the San Francisco Bay area over the time period 1995 through 2015.

Ventura and Ojai. However, more sampling in the area may reveal a connection for gene flow between the two areas.

Observations of the EFS began to occur in Orange County in the late 1990s and early 2000s. At that time, the front of range natural range expansion was in the northern portions of Orange County but isolated pockets of the EFS were present in Costa Mesa and Irvine, most likely due to introduction by humans. Less than 20 yrs later the species can be found throughout much of Orange County (Fig. 5) with the species now wide-spread as far south as Huntington Beach and Irvine. The gap in distribution that was present due to the establishment of the isolated populations in Costa Mesa and Irvine is now gone as animals have dispersed eastward from the contiguous front of range expansion in 2004 and in all directions from the isolated, human-established populations. Single observations have been reported in Laguna Beach and Lake Forest. Some undeveloped land in the southeastern portion of Irvine, as well as a geographic constriction of developed land between the Santa Ana Mountains and the coastal mountains may slow range expansion to the southeast for a time. However, potentially suitable but now

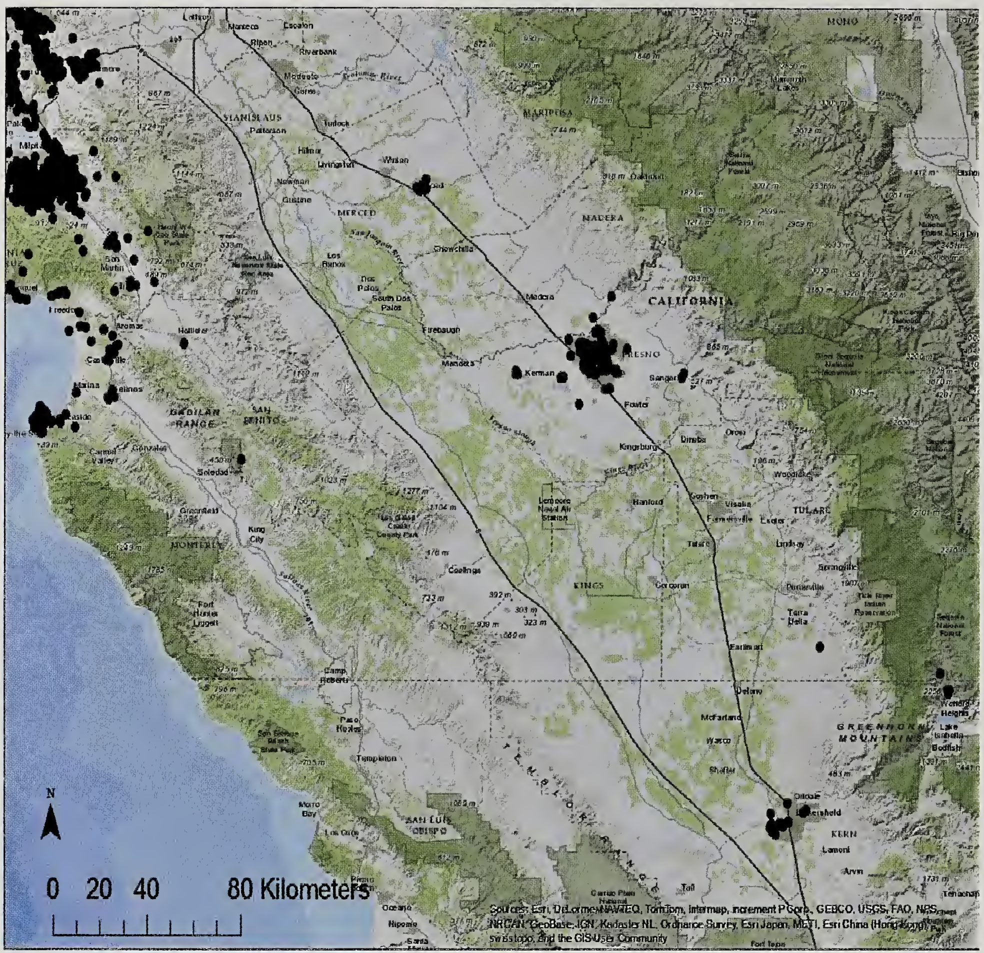

Fig. 4. Observations of the Eastern Fox Squirrel, *Sciurus niger*, in the southern portion of the Central Valley area of California over the time period 1995 through 2015.

unoccupied habitat is plentiful south of Irvine in cities such as Mission Viejo, Laguna Niguel, San Juan Capistrano, Dana Point, and San Clemente.

While the EFS has been present in the City of San Diego for almost 100 years, range expansion appears to have been extremely limited over this time period. Most observations have been in the area around Balboa Park adjacent to the San Diego Zoo and within a few km of the original site of release. Animals introduced to the Stockdale Country Club in Bakersfield have spread throughout much of that city and animals introduced to Kernville, in addition to spreading through much of the small town, have also dispersed north along the Kern River toward the Sequoia National Forest (Fig. 4).

Data from several regions allowed an estimate of the maximum straight-line distance (MSLD) of range expansion since introduction to a particular location. In southern California, the MSLD from the Veterans Hospital in Los Angeles (introduction 1904) to near Interstate 15 in Rancho Cucamonga (84 km) gives a rate of 0.8 km/yr while the distance from the Veterans Hospital to Lake Forest (85 km) also gives a range expansion rate of 0.8 km/yr. The MSLD from Sacramento to Auburn of 50 km (introduction to Sacramento in 1921) gives an expansion rate of 0.5 km/yr

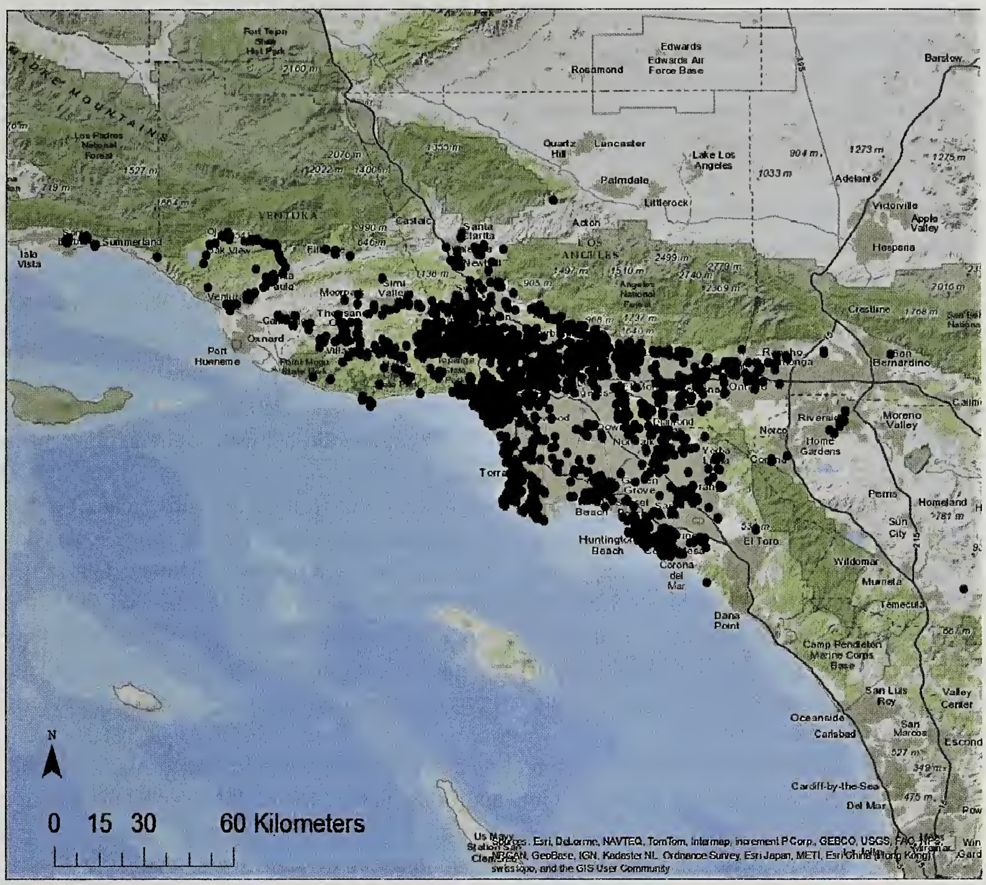

Fig. 5. Observations of the Eastern Fox Squirrel, *Sciurus niger,* in the Los Angeles metropolitan area north to Santa Barbara over the time period 1995 through 2015.

while a MSLD of 64 km from Sacramento to Placerville gives a rate of 0.7 km/yr. Using 1890 as an introduction date to Golden Gate Park in San Francisco, although the introduction may have been before 1890, the MSLD to Salinas of 145 km gives an expansion rate of 1.2 km/yr. The MSLD from Stanford University (introduction 1921) to Salinas is 95 km giving a rate of 1.0 km/yr.

Discussion

As we have shown, the EFS has greatly expanded its range within California from points of initial introduction. Although the species is mainly observed at this time within urban and suburban areas of California, animals have also been observed in rural areas (west and east of Fresno) and in areas of native range of California (along the south fork of the American River near Coloma and in areas around Grass Valley in the foothills of the Sierra Nevada Mountains). The EFS is an agricultural pest in almond and fruit orchards west of Fresno and the dispersal of animals along major waterways such as the American, Kern, King, and Sacramento Rivers has allowed the species to occupy areas of native range away from human habitation. The EFS is now located in regions where invasion of habitats within the Sierra Nevada Mountains, as well as other mountain ranges within the state is possible. An important question to ask is how far from urban and suburban areas the EFS will expand its range.

The EFS is a generalist species (Koprowski 1994) typically found within its native habitat in upland forested areas, open forests, riparian areas, residential areas, or areas neighboring open spaces such as agricultural lands and pastures containing trees. The EFS is able to live in large numbers in areas with high tree diversity (Nixon and Hansen 1987) and they are also more tolerant than some other species of low tree density (Wolf and Roest 1971). The EFS has a higher reproductive output than the WGS with adult females capable of producing litters twice per year with an average litter size of two to three pups (Koprowski 1994). Breeding generally occurs November-February and April-July (Brown and Yeager 1945; Moore 1957). The EFS is also more generalist than the native WGS in food choice (King 2004; Ortiz and Muchlinski 2015). The above referenced natural history traits may allow the EFS to displace the native WGS in certain habitats (Muchlinski et al. 2009; Cooper and Muchlinski 2015).

Some reasons for differences in the rate of range expansion by tree squirrels have been suggested by Signorile (2014) and include size of the founding population, genetic diversity and population structure. Larger sizes of founding populations were associated with greater genetic diversity, more dispersal, less local genetic differentiation and faster rate of range expansion rate in squirrels. The rates of long-term range expansion between 0.5 and 1.2 km/yr determined from this study are less than the 1.5 km/yr determine by Garcia and Muchlinski (2017) in highly suitable suburban habitat. As the EFS expanded its range over many decades it may have encountered habitats, which were not highly suitable at one time but highly suitable at a later date, thereby decreasing the long-term rate of range expansion in comparison to shorter term rates in highly suitable habitats.

It is very likely that the EFS will continue to expand its range within California, especially in human-developed areas and potentially into additional natural habitats. With continued range expansion of the EFS there may be additional impact on the native WGS, especially in lowland habitats (Cooper and Muchlinski 2015). However, in areas of California where the EFS is now sympatric with the invasive eastern gray squirrel, *Sciurus carolinensis* (EGS), or may become sympatric with the EGS, the EFS may experience contraction in geographic range or in population size (Creley and Muchlinski 2017). The EGS is spreading rapidly in many areas of central California so continued assessment of the relationship between the EFS, the WGS, and the EGS within California is warranted.

Acknowledgements

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Distribution of the Eastern Gray Squirrel (*Sciurus carolinensis*) within California as of 2015

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Abstract.—The goals of this study were to map the distribution of the invasive eastern gray squirrel, *Sciurus carolinensis*, in California as of 2015 and to assess range expansion since the first documented sightings within the state. Range maps exist, but the last update by the California Department of Fish and Wildlife was in 2007. An assessment of the rate of range expansion over time has not been conducted, but comparisons between the locations of initial sightings and the current distribution are included. Location data were obtained from museum specimens, wildlife rehabilitation centers, a roadkill database, and research-grade citizen observations. Range maps were produced with ArcGIS software. Populations of eastern gray squirrels are currently concentrated around Sacramento and Davis, the western side of San Francisco Bay, within as well as north and east of Santa Cruz, within Monterey, north of the Golden Gate Bridge through Marin County as well as around Santa Rosa, and around the Bellota/Stockton area. Isolated populations on the eastern side of San Francisco Bay occur around Berkeley, Hayward, and Pleasanton. Observations extend into the foothills of the Sierra Nevada Mountain Range from north of the American River to south of the San Antonio River. We suggest that the eastern gray squirrel might become more damaging to the two native diurnal species of tree squirrels in California, *Sciurus griseus* and *Tamiasciurus douglasii*, than the introduced eastern fox squirrel (*Sciurus niger*).

The eastern gray squirrel, *Sciurus carolinensis* (EGS), is a medium sized tree squirrel with a total length of 380-525 mm, and adult body mass from 300 to 700 g (Barkalow and Shorten 1973; Hall 1981). Its congeners are the eastern fox squirrel, *Sciurus niger* (EFS), which is greater than 20% larger in body size (McGrath 1987), and the western gray squirrel, *Sciurus griseus* (WGS), which is slightly longer in total length (Koprowski 1994). The EGS has a gray dorsal pelage and white tipped guard hairs that are never tawny, brown, or orange (Koprowski 1994). Unlike the WGS, which has a uniformly gray body and pure white underside, the EGS may have a cinnamon wash on the hips, feet and head, buff to gray to white on the ears, and gray to buff to cinnamon underside (Flyger and Gates 1982).

The EGS is native to the deciduous forests of the eastern United States and southern Canada from Saskatchewan to North Dakota, south to eastern Texas, east to Florida, and throughout Quebec and Maine (Koprowski 1994). The EGS's original native range consists of mature, continuous woodlands over 40 ha in size, with diverse woody understories and tree species such as oak (*Quercus*), hickory (*Carya*) and walnut (*Juglans*). However, the EGS can also live in urban and suburban environments, even with relatively few mature trees (Thorington et al. 2012).

Extant populations of the EGS are located in central California, with populations spreading and growing since their introduction. The earliest recorded sighting of the EGS in California occurred in 1900 at Golden Gate Park in San Francisco. Specimens were collected in 1921 at Stanford University in Palo Alto. The first specimen collected from the city of Santa Cruz was in 1938. By 1940 the species had spread west from Palo Alto to the eastern edge of the Santa Cruz Mountains and by 1946 specimens were collected within the Santa Cruz Mountains. The species had also spread north from Palo Alto to Redwood City by 1948. The species was introduced to the Capitol Mall in Sacramento in 1973, and populations were identified in Pleasanton, as well as in a region called Bellota, an area within San Joaquin County along the Calaveras River, in 1974 (Byrne 1979).

The species may have been introduced to large estates as early as the 1860s in an effort to create park like grounds similar to those found on the east coast (Byrne 1979). Specimens from California are probably underrepresented in museum collections because of the species' recent colonization of the state. The California Department of Fish and Wildlife last updated its range map for the EGS in California in 2007. The existing data is insufficient to complete a study on the rate of range expansion of the EGS in California, but a general assessment is made of the species' spread over time.

Invasive populations of the EGS have been associated with negative ecosystem effects including the decline of native species and damage to forests in the United Kingdom, Ireland, Italy, and parts of western North America (Benson 2013; Bertolino 2008; Bertolino and Lurz 2013; Gurnell et al. 2004). The EGS threatens native species and habitats because of its ability to live and reproduce in a wide range of urban, suburban, and natural habitats, its broad diet (Bertolino 2008), its high reproductive rate, and its ability to establish a population from a small number of founders (Wood et al. 2007). External effects that are occurring simultaneously with the invasion, such as habitat fragmentation, changes in forest structure, the spread of other invasive species, and the species' favorable public perception (Bertolino and Genovesi 2003) contribute to its invasive ability.

Materials and Methods

Location data gathered from within California between January 1900 and the end of August 2015 were used for this study. Museum records were collected from iDigBio, the Global Biodiversity Information Facility (GBIF), and Vertnet. Since specimens of invasive species such as the EGS are very limited in museum collections, other sources of location data were needed for this study. Of the 3,633 observations of EGSs, 78% were obtained from wildlife rehabilitation centers. Some rehabilitation centers were able to provide detailed intake records from 2005 through 2015, while other centers could only provide records for a more limited number of years. Records from wildlife rehabilitation centers are concentrated around the area of their geographic locations, and this may lead to an overrepresentation of location records from residential areas surrounding the center. Intake records from these centers show the location from which the squirrel was collected by the person who dropped the squirrel off at the rehabilitation center. Geographical bias related to records from wildlife rehabilitation centers would come from most centers being located in urban/suburban areas. We used only records that included information that could be traced to a specific street address or intersection within a specified city.

Additional sources of data included: The California Department of Public Health's West Nile Virus Surveillance Program; the California Roadkill Observation System, operated through the University of California, Davis; research grade human observations from iNaturalist; and observations by Alan Muchlinski and graduate research students from California State University, Los Angeles. Research grade iNaturalist data include a date of observation, photo, as well as latitude and longitude coordinates, and the species has been corroborated by at least one additional user.

Since some misidentifications were likely to be present in all of the sources of data, field surveys were conducted in selected regions of California and observation reports of the EGS outside of the previously reported distribution were scrutinized for accuracy. Field surveys were conducted in parts of the Santa Cruz Mountains, the Central Valley, and southern California. Records from areas where the species was not thought to occur currently or historically were investigated, and if the species was not found, the records were expunged from this study. Biodiversity databases are constantly changing as records are added from existing databases and erroneous records are erased. The location data from iDigBio, GBIF, and Vertnet used in this paper were accessed on 31 August 2015. Although use of multiple databases may result in some redundancy of location points, this does not change the overall distribution of the species.

Observations obtained through iNaturalist are utilized under a Creative Commons By Attribution Non-Commercial License or from observations that are in the Public Domain. The Global Biodiversity Information Facility is an international open data source. VertNet is a National Science Foundation funded project that makes museum-curated biodiversity data free and available on the web. Names of contributors to GBIF and iNaturalist can be obtained through a search using the data posted at DOI: 10.13140/RG.2.2.21869.59367. Data used in this manuscript are available for use by others under a Creative Commons By Attribution Non-Commercial 4.0 International License.

The mapped results are presented at different landscape levels, including various regions of the state. Individual sighting data that were submitted as addresses or location descriptions were converted to geographic coordinates using Google Maps. The coordinates and corresponding information related to species identification, the date of the observation, and additional information were saved as a comma-delimited file. Location data for the EGS were added to ArcMap 10.3.1 and projected to the NAD 1983 California (Teale) Albers (Meters) data frame coordinate system because that is the preferred projection of the California Department of Fish and Wildlife.

Inconsistent data recording and collection over time make it impossible to calculate the rate of spread of the EGS in California. Data were collected in bursts from different sources. For example, from 1900 to 1969, most records are from museums. In the 1970s a large number of Vertnet records were provided by Sheila Byrne (Byrne 1979). From 2004 – 2015 most of the records are provided by wildlife rehabilitators (Table 1).

Results

The overall distribution of the EGS within California is depicted in Fig. 1. One population of EGSs is located on the southern peninsula of San Francisco Bay, from San Francisco south to areas around Gilroy and Santa Cruz (Fig. 2). Sightings have not been reported that directly connect animals in Gilroy with animals in Santa Cruz, without heading north to the main body of the distribution near San Jose. The population is highly concentrated within urban and suburban areas of San Francisco, San Mateo, Santa Cruz and Santa Clara Counties, and the population follows developed areas along the Highway 101 corridor to the southern edge of Santa Clara County. The species has been observed in forested mountain habitat away from urban/suburban areas (Fig. 2), and could be more widely distributed within large tracts of redwood forests in areas such as Big Basin Redwoods State Park and Henry Cowell Redwoods State Park. EGSs were observed within both parks by co-author AEM so more investigation of the distribution of the EGS in these areas is warranted. This population is positioned to expand north into developed areas along the eastern side of San Francisco Bay by wrapping around the bay from the areas near San Jose.

Table 1. Sources of observations of the EGS, *Sciurus carolinensis,* within California from 1900 through 2015.

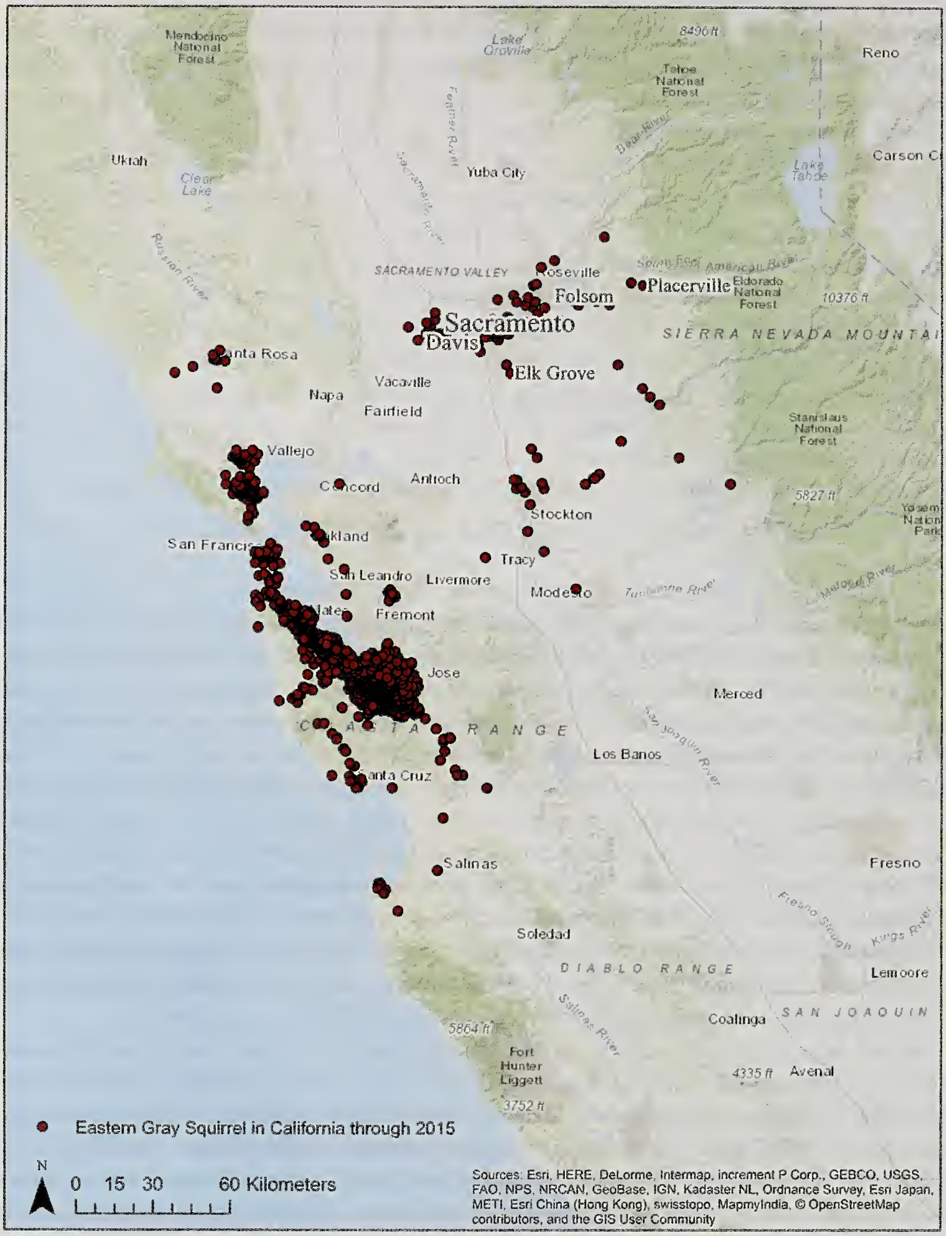
Sources of observations from 1900 - 2015	Records
California Department of Public Health	154
California State University, Los Angeles	27
Global Biodiversity Information Facility	39
iDigBio	17
iNaturalist	209
Lindsay Wildlife Experience	23
Peninsula Humane Society	756
Society for the Prevention of Cruelty to Animals, Monterey County	7
Sonoma County Wildlife	1
Stanislaus Wildlife Care Center	7
Sulphur Creek Nature Center	6
UC Davis, California Roadkill Observation System	122
Vertnet	239
WildCare Rehabilitation Center	334
Wildlife Center of Silicon Valley	1,692
Total observations in California	3,633

Another large area occupied by EGSs is present within the city of Sacramento, west to Davis, east to areas around Placerville, south along the foothills of the Sierra Nevada Range, and then west to areas around Modesto and areas west of Stockton (Fig. 3). Sightings on the eastern edge of the distribution range along California Highway 49 from south of the town of San Andreas on the south to near Interstate Highway 80 on the north, while the western edge runs from around Manteca on the south to Davis on the north. Sightings along the northern edge of the distribution follow Interstate 80 from Davis, through Sacramento, past Roseville north of Folsom Lake State Recreation area, along U.S. 50 through Folsom, into the El Dorado Hills and into areas around and north of Placerville. Whether there is a continuous connection to form one single population or whether there are separate northern and southern populations within this overall area (Fig. 3) is uncertain at this time. Animals in the northern part of this region may have originated from the population established at the Capitol Mall in Sacramento while animals in the southern part of the region may have originated from the population established around Bellota.

Several more apparently isolated populations exist within the state. One apparently isolated population exists on the Monterey Peninsula (Fig. 2). This population ranges from the northern tip of the Monterey Peninsula south to the Carmel River and inland to Salinas, although it is unknown if there is a direct connection between animals around Monterey and those within Salinas (Fig. 2). The lack of sightings directly between Santa Cruz and Gilroy as well as between Monterey and Salinas could be because the land is largely agricultural and unsuitable for tree squirrels, or because the area is highly rural and no sightings have been reported.

Isolated populations now exist north of the Golden Gate Bridge within Marin and Sonoma Counties. The first EGS reported by WildCare Rehabilitation Center, approximately 16 km north of the bridge, was in 2005, indicating the species most likely arrived in the area within a decade prior to 2005. One population occupies an area from Sausalito on the south, along the Highway 101 corridor, through San Rafael, to around Novato on the north, while the second population is located within the city of Santa Rosa, west to Sebastopol, and south to Rohnert Park. It is uncertain if these two populations have merged into one population at this time.

Isolated populations of the EGS are now found on the eastern side of San Francisco Bay in two locations. One population, first recorded in 1974, is located around Pleasanton, a city located



Sources: Esri, HERE, DeLorme, Intermap, increment P Corp., GEBCO, USGS, FAO, NPS, NRCAN, GeoBase, IGN, Kadaster NL, Ordnance Survey, Esri Japan, METI, Esri China (Hong Kong), swisstopo, MapmyIndia, © OpenStreetMap contributors, and the GIS User Community

Fig. 1. Range Map of the eastern gray squirrel within California as of 2015. Reported observations of eastern gray squirrels are shown as points.

east of the Coastal Range and west of Livermore, CA. A second population appears to occupy an area from Berkeley south to Hayward, mostly along the edge of the bay (Fig. 2). The first intake records for EGSs from Sulphur Creek Nature Center (SCNC) in Hayward are from 2009, indicating relatively recent occupation of habitat south of Oakland on the western side of the Coastal Range. The full extent of the population in and around Hayward is not known as SCNC

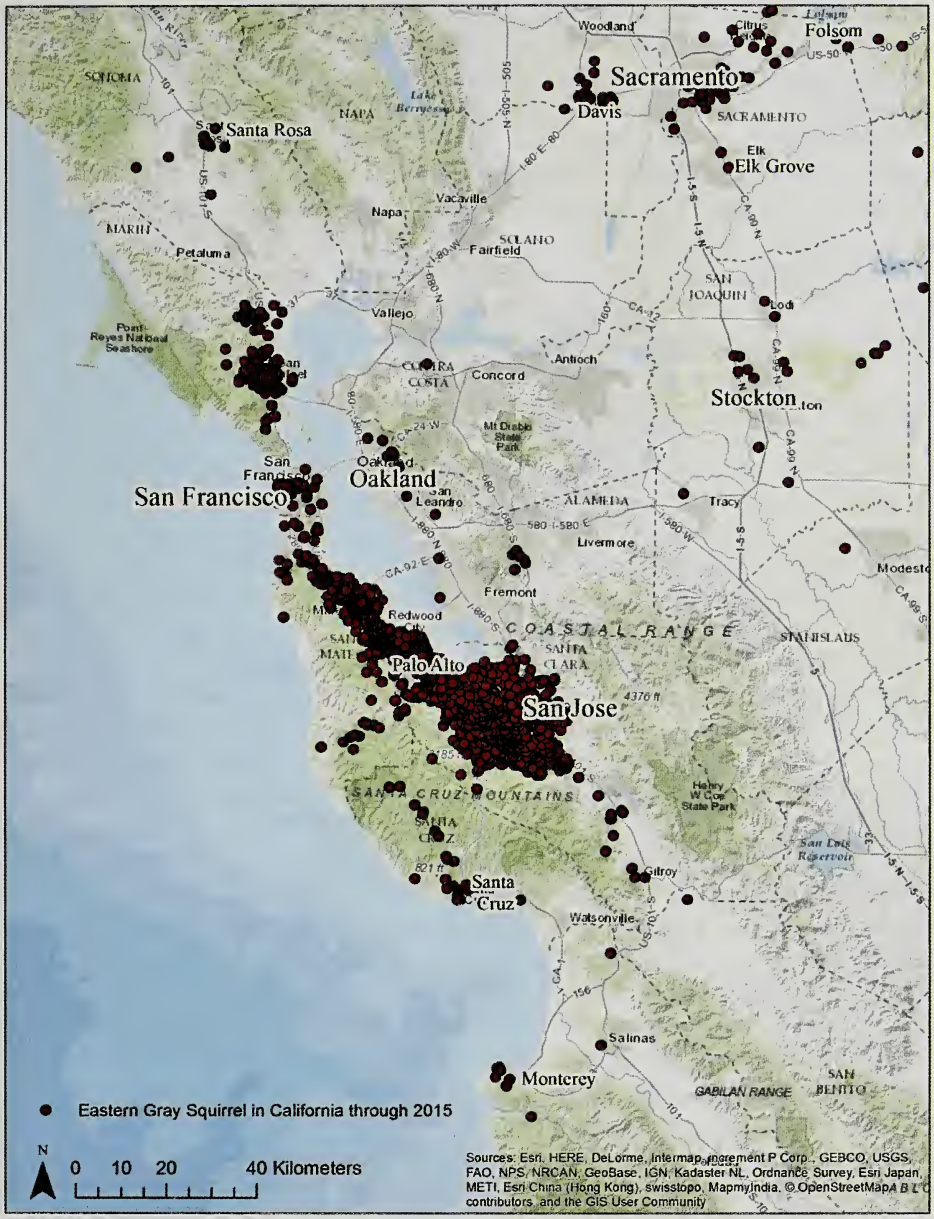


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Fig. 2. Location map of the eastern gray squirrel on and around the San Francisco Bay as of 2015. Reported observations of eastern gray squirrel are shown as points.

is funded by the City of Hayward and only takes in animals from the immediate surrounding area. However, EGSs seem to be much less abundant in the area at this time than EFSs. While 173 EFSs were taken in by SCNC between 2009 and 2013, only 9 EGSs were taken in over the same time period. At this time the EGS is greatly outnumbered by the EFS on the eastern side of San Francisco Bay.

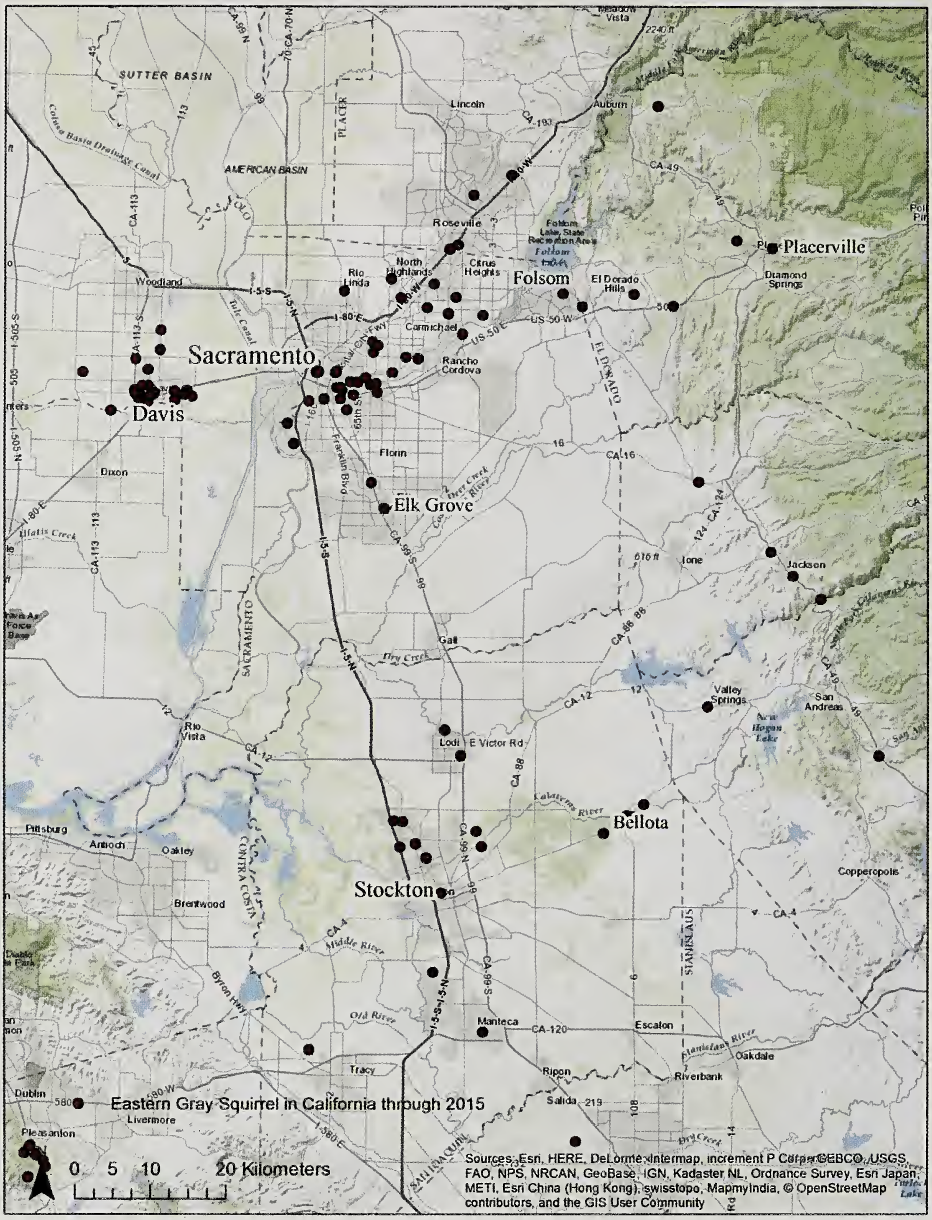

Fig. 3. Location map of the eastern gray squirrel around Sacramento and the Central Valley. Reported observations of the eastern gray squirrel are shown as points.

Discussion

The EGS is now well established in California and has expanded its range considerably since initial introductions. The EGS could affect populations of both native diurnal species of tree squirrels within California and it may be associated with changes in populations of the other introduced tree squirrel species in California, the EFS.

Populations of the Douglas squirrel, *Tamiasciurus douglasii*, (DS) are found in coniferous forests within the coastal mountain range in the northwestern region of California as well as at high elevations within the Sierra Nevada Mountains (Storer et al. 2004). Secondary habitats include hardwood and shrubby wetlands, conifer-hardwood forests and riparian habitats (Brown 1985, Zeiner et al. 1990). Replacement of the DS by the EGS in Vancouver, Canada has been in mixed hardwood habitat, not within coniferous forests (Hwang and Larivière 2006). Replacement of *Tamiasciurus hudsonicus* (American red squirrel) by the EGS on Vancouver Island, Canada has also been primarily in mixed-hardwood forests (Bruemmer et al. 1999). Coniferous forests dominated by pine, spruce and fir trees could be unsuitable habitat for the EGS in California. However, EGSs have been sighted by co-author AEM in redwood forests within Henry Cowell and Big Basin Redwoods State Parks between Santa Cruz and San Francisco. Future contact zones between the DS and the EGS near redwood forests should be monitored as should contact zones between the DS and EGS in mixed hardwood-conifer forests.

Replacement of the European red squirrel, *Sciurus vulgaris* by the EGS in mixed hardwood forests has occurred across most of Britain. However, the pattern of introductions of the EGS into and within California has been very different than introductions into and within Britain. Approximately eight introductions occurred into mainland areas of California, including areas around Bellota, Marin County, Monterey, Palo Alto, Sacramento, San Francisco, Santa Cruz, and Santa Rosa. Over 30 introductions and translocations of the EGS into and within Britain occurred mainly to large estates in rural areas between 1876 and 1930 (Middleton 1930). The mixed hardwood forests within these rural areas provided good habitat for the EGS. Other translocations within Britain likely occurred since 1930 along with rapid spread of the species across England, Scotland, and Wales in the mid-1900s (Shorten 1953). Continued range expansion by EGSs that now exist within Marin and Sonoma Counties into secondary habitats of the DS in the coastal mountain range could affect some populations of the DS in a manner similar to how the EGS has displaced *S. vulgaris* in parts of Great Britain. Therefore, monitoring of future contact zones is encouraged.

The EGS is a more generalist species than the WGS (Carraway and Verts 1994; Koprowski 1994), so it may pose a threat to the WGS as it continues range expansion within California. The EGS's original native range consists of mature, continuous woodlands over 40 ha in size, with diverse woody understories. However, EGSs can also live in urban and suburban environments, even with relatively few mature trees (Thorington et al. 2012). Habitat fragmentation poses a significant threat to WGSs but favors EGSs. WGSs can sometimes be found in cities or agricultural nut orchards, but are much more common farther from human development (Thorington et al. 2012), whereas the EGS is more tolerant of habitat fragmentation (Moore and Swihart 2007). In fragmented habitats, the EGS increases in density and reduces its home range, as long as it has a minimum patch size (Koprowski 2005). EGSs are capable of living in forested areas similar to those inhabited by the WGS. EGSs may pose a greater threat to the native squirrels than the EFS because although EFSs are similarly tolerant of habitat fragmentation (Moore and Swihart 2007)the EFS is more limited to areas with low ground cover (Gatza 2011). EGSs are capable of living in diverse habitats including forested mountains, so they may be capable of expanding to areas that EFSs cannot reach.

Finally, the EGS may be affecting populations of the invasive EFS within California. The EGS may be replacing the EFS along the western side of the San Francisco Bay in California. Although intake records have some geographic bias, an almost complete replacement of intake specimens of the EFS by specimens of the EGS submitted to two wildlife rehabilitation centers suggest that a replacement of the EFS by the EGS is occurring in these two locations. Intake records from Peninsula Humane Society Rehabilitation Center in Burlingame, California (approximately half-way between San Francisco to the north and San Jose to the south) from 1975 show 0% (0) EGSs and 100% (152) EFSs. In 2013 intake records show 99.5% (405) EGSs and .5% (2) EFSs. Intake records from the Wildlife Center of Silicon Valley, located in San Jose, for 2004 show 60.5% (69), EGSs and 39.5% (45) EFSs, while in 2012 intake records show 87.2% (157) EGSs and 12.8% (23) EFSs. The EGS also replaced the EFS in the 1960s and 1970s in a new subdivision in St. Louis County, Missouri (Sexton 1990). As the EGS is positioned to invade the eastern side of San Francisco Bay from both the northern and southern sides, and isolated populations currently exist on the eastern side of the bay, there could be a decrease in the EFS population in this area and an increase of the EGS over time.

Conclusions

We suggest that the EGS might become more damaging to the two native diurnal species of tree squirrels in California (*Sciurus griseus* and *Tamiasciurus douglasii*) than the introduced EFS (*Sciurus niger*). The EGS currently occupies habitats within urban and suburban areas of the state and is encroaching into forests in California. Populations of the EGS are widespread throughout the southern peninsula of the San Francisco Bay, the northern peninsula of the San Francisco Bay, and San Jose. Smaller populations are located in Santa Cruz, spreading into the Santa Cruz Mountains, and on the Monterey Peninsula. In the Central Valley, populations exist in and around Sacramento, Davis, Placerville, Modesto, Stockton, and along the foothills of the Sierra Nevada Range. Populations have spread near undeveloped forested areas of the state as well as into additional human-developed regions. Careful attention should be paid to continued range expansion of this species.

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Status of the Isolated, Threatened Valle de la Trinidad Round-Tailed Ground Squirrel, Baja California, Mexico

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The round-tailed ground squirrel (*Xerospermophilus tereticaudus*) is a diurnal rodent adapted to a wide range of arid environments of the southwestern U.S. and northwestern Mexico. Along the western margin of its range some populations have been historically isolated in valleys, and have been distinguished as distinct subspecies. One such population, historically isolated from the continuous range of the species, has been restricted to suitable habitat in the Valle de la Trinidad region, Baja California, west of the Sonoran Desert (Hall 1981). Nelson and Goldman collected the first specimens from this population during a brief visit in 1905, but not until Huey did further collecting and taxonomic analysis, was this population named as a different subspecies, the Valle de la Trinidad round-tailed ground squirrel, *X. t. apricus* (Huey 1927). The range of this subspecies has been usually considered as geographically unconnected from that of other subspecies (Ernest and Mares 1987; Huey 1964), but Hafner et al. (1998) suggest that it was connected through the Arroyo de San Matías, which leads from Paso de San Matías to the desert floor (Fig. 1). We surveyed this wash in 2015 and found suitable habitat to be sparse with no round-tailed ground squirrels present, and concluded that the Valle de la Trinidad and Sonoran desert populations were not connected.

Valle de la Trinidad, as defined by Huey, is an isolated valley, measuring roughly 6 × 30 km, which lies between two mountain ranges, Sierra de Juárez to the north and the Sierra de San Pedro Mártir to the south. Whereas Huey and other U.S. writers have considered the whole area as Valle de la Trinidad, in Mexico it is considered as two valleys. Valle de la Trinidad, is on the western side and has been extensively transformed by agriculture. Valle de San Matías, on the eastern side, consists of higher ground less suitable for farming, but used as cattle range (Fig. 1).

No data are available on the habitat prior to the onset of cattle ranching in the region, but Lawrence M. Huey (6 July 1927 field notes) recorded at Newhouse's ranch that "... [at] the western end of the valley ... a permanent stream of water flows. Here also the heaviest growth of mesquites occurs." About 5 km east, on the north side of the valley, Huey noted that conditions were "vastly different" and "Creosote [*Larrea tridentata*] proved to be the most common shrub with Squaw Tea [*Ephedra* sp.] and Catclaw [*Senegalia greggii*] as close seconds." Mesquites (*Prosopis glandulosa*) were scattered and not abundant. It is likely that such shrubs in the area, especially the mesquites, had increased since contact time, promoted by cattle grazing, as has been documented elsewhere (Mellink and Contreras 2014). Currently the Valle de la Trinidad

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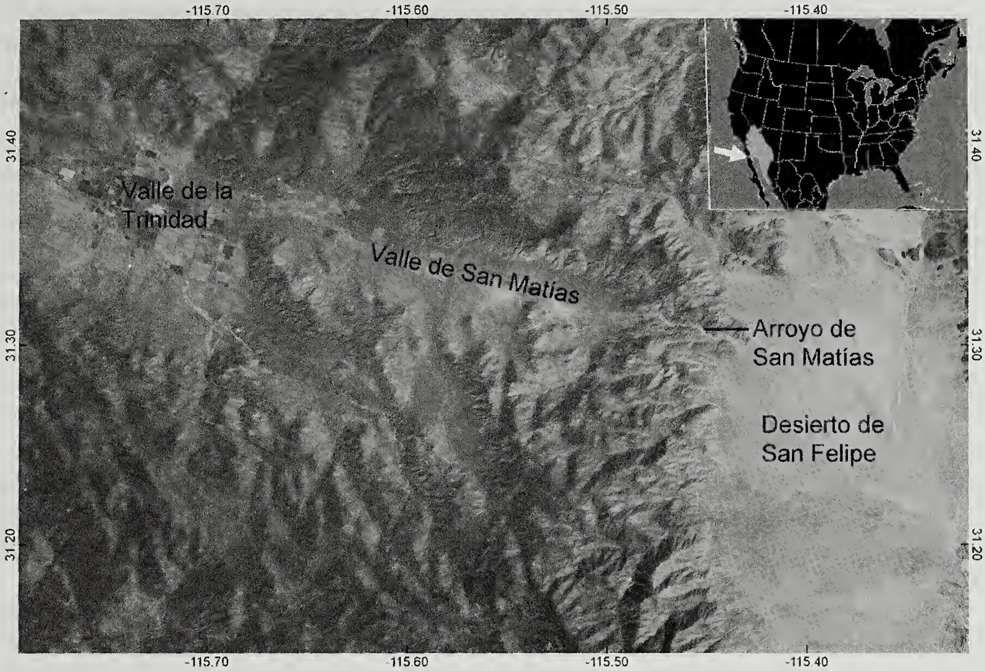

Fig. 1. Study área. In older literature, often both valleys, de la Trinidad and San Matías, have been considered under a single name, "Valle de la Trinidad". Species distribution (light gray) insert from: https://naturalhistory.si.edu/mna/full_image.cfm?image_id=1179. White arrow indicates the range of *the* Valle de la Trinidad round-tailed ground squirrel.

proper is widely farmed, but in the Valle de San Matías vegetation is similar to that described by Huey in 1927.

Huey found round-tailed ground squirrels to be abundant at his two survey sites, in Valle de la Trinidad proper, were he collected several specimens. Other collectors also collected on the western side. Later, two 1979 specimens from "East Valle de la Trinidad" (SDNHM mammal collection) could have been from Valle de San Matías, but this is unclear. In 2010 E. Mellink and J. Luévano surveyed Valle de la Trinidad extensively and found only two individuals, next to the cemetery among mesquites and creosote bush. They found none on return visits. Low success by Mellink and Luévano in their 2010 surveys generated fears that the subspecies could be extinct. Thus, in order to find out the status of this population, we carried out extensive field work in 2015 in and around Valles de la Trinidad and San Matías.

Pelage color of round-tailed ground squirrels allow them to blend with the light desert soils on which they live, making them difficult to detect visually unless they run. However, they emit a distinctive, high-pitched birdlike "peeeeet" call, which allows for reliable acoustic surveys. We combined visual and auditory detection along transects through patches that conformed to known preferred habitat and different habitat patches. In the spring and summer of 2015 we surveyed 456 points, spaced about 200 m along 28 transects that ended usually after the habitat was clearly unsuitable. At each point we observed and listened for 3 minutes. Each point was surveyed once. Most detections in our surveys were auditory, and whenever possible, triangulation of a call allowed for identification of an individual. As it can be difficult to determine precisely how many squirrels were calling, we recorded relative abundance as: not detected; low = 1–2 individuals; medium = 3–5, or high ≥ 5. At each point we recorded habitat

Table 1. Number of points surveyed for the presence of Valle de la Trinidad round-tailed ground squirrel on different dates, points at which it was detected, and groups sizes at detection (low = 1-2 individuals; medium = 3-5, or high = >5).

			Group size		
Date	# of points	Points with detections	Low	Medium	High
28-04-15	39	20	4	2	1
29-04-15	15	11	6	3	2
06-05-15	6	3	2	1	0
16-05-15	28	14	13	1	0
10-06-15	104	52	51	1	0
11-06-15	107	95	95	0	0
30-06-15	23	0	0	0	0

characteristics (topography, soil type, vegetation type, percent bare ground), and land use (active agriculture, fallow, range, housing, other). Our procedures conformed to published American Society of Mammalogy guidelines for the use of wild mammals in research, and to official Mexican requirements.

We obtained positive presence records at 195 different points (Table 1, Fig. 2). All positive presence points were in Valle de San Matías, and none in Valle de la Trinidad proper. No individuals were found in the area were EM and JL had documented the species in 2010, in

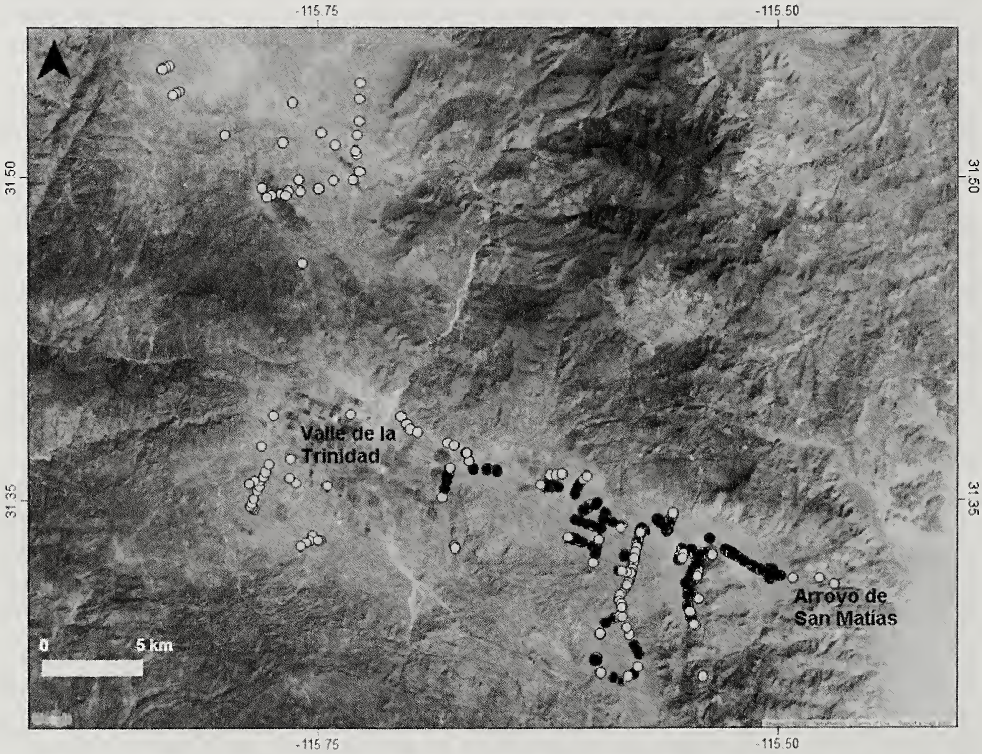

Fig. 2. Presence (black dots) and no detection (white dots) of round-tailed ground squirrels in Valle de la Trinidad – Valle de San Matías and nearby areas, Baja California, Mexico. 2015.

Table 2. Number of points surveyed for the presence of Valle de la Trinidad round-tailed ground squirrel according to habitat, points at which it was detected, and groups sizes at detection (low = 1-2 individuals; medium = 3-5, or high = >5).

			Number detected		
Habitat	# of points	Points with detections	Low	Medium	High
Mesquite with scrub, actual grazing	7	0	0	0	0
Mesquite with scrub, little actual grazing	123	108	108	0	0
Mesquite without scrub, little actual grazing	24	19	18	1	0
Plowed agriculture	1	1	1	0	0
Fallow	10	8			

Valle de la Trinidad. Most individuals were found in open mesquite communities on sandy soils (Table 2). Although most points with positive detections were in areas that exhibited little presence of cattle at the time of our surveys (Table 2), the entire area has a long history of grazing.

Agreeing with the species preference for mesquite scrub woodland with herbaceous native desert plants, we found most individuals in open communities of large leguminous trees or shrubs, principally mesquite. We repeatedly observed the species feeding on the seed pods and flowers of mesquite, and inferred these to be critical seasonal components of the diet, especially as no other food plants were available at several sites. It is not clear to what extent grazing has degraded this landscape, but the presence of non-native annual grasses (predominantly *Schismus barbatus*) suggests some history of intensity of grazing. Before grazing, this habitat may have had quite different soil properties and cover (*sensu* Mellink and Contreras 2014). We found the squirrel to be denser in areas with some disturbance from cattle and/or yucca (*Yucca schidigera*) extraction, suggesting an association with soil disturbance.

From our survey, the currently known geographical distribution of the Valle de la Trinidad round-tailed ground squirrel is restricted to Valle de San Matias. The points at which we recorded the subspecies extend in elevation from 760 to 1,100 m. The presence of a dominant perennial legume, particularly mesquite, appears to be a preference for this species' distribution in this area. This is similar to what happens in San Felipe and Laguna Salada populations, in the Sonoran plain to the east, where we detected very few round-tailed ground squirrels in areas without leguminous trees (unpub. obs.). The persistence of the Valle de la Trinidad round-tailed ground squirrel might depend on the continued presence of dominant legumes in these rangelands, and habitat connectivity throughout the valley.

Although round-tailed ground squirrels are found in agricultural context both in Imperial Valley and Valle de Mexicali, as well as in Arizona and Sonora, they do not occur in the Valle de la Trinidad farmland. Anthropogenic activities that may have caused this include the type of crop produced and possibly pest control. The alfalfa grown in the past may have favored the round-tailed ground squirrel as it does in Valle de Mexicali and Imperial Valley, as well as in Sonora (E. Mellink, N. Siordia and S. Tremor, unpub. obs.; see also Drabek 1970). However, the shallots and other crops grown today seem unfavorable. Conversion to cultivation in greenhouses eliminates habitat for the squirrel and creates barriers that may result in habitat fragmentation. Although some uncultivated patches with mesquite vegetation remain between farmed plots in Valle de la Trinidad, round-tailed ground squirrels are not in them. It is possible that these patches are too small and, or the squirrels were locally extirpated by agricultural pest control activities; and isolation from the current colony prevents their recolonization. Our field work allows us to conclude that: (i) the Valle de la Trinidad round-tailed ground squirrel is not extinct, (ii) this small, single population is vulnerable to extinction from future agricultural expansion eastward and use of pesticides, (iii) the remaining population warrants formal protection and, (iv) reintroduction of squirrels to patches where they were apparently extirpated should be considered, along with habitat restoration if needed.

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Reproductive Morphology of Male Black Perch (*Embiotoca jacksoni*)

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The surfperches (Embiotocidae) are comprised of 24 species, all but one species is marine and they range from central Baja California to Alaska (not including the Aleutian Islands) and Japan in the Pacific Ocean (Baltz 1984; Holbrook et al. 1997; Longo and Bernardi 2015). Embiotocids occupy various marine habitats including sandy bottoms, rocky reefs, kelp forests, and seagrass beds (Allen and Pondella 2006). The tule perch (*Hypsterocarpus traskii*) is freshwater and occupies lakes and rivers in central to northern California (Baltz and Moyle 1982; Wang 1986).

The surfperches are among approximately 500 fishes that exhibit internal fertilization and bear live young (Contreras-Balderas 2006). During copulation, male surfperches utilize external copulatory structures (e.g., genital papilla, intromittent organs) to transfer sperm into the female reproductive tract (Blake 1868; Hubbs 1917; Tarp 1952; Gardiner 1978). Sperm are transferred in a mass, which contains spermatozoa from multiple lobules (Gardiner 1978; Grier et al. 2005). The sperm mass of surfperches has been referred to as a spermatophore in previous literature (Shaw and Allen 1977; Gardiner 1978). It should be noted however, that the term spermatophore refers to a package of sperm which is encapsulated by an extracellular capsule (Ginzburg 1968; Wourms 1981). In embiotocids, the spermatozoa come together to form large aggregates called spermatozeugmata, which are not enclosed by a membrane (Ginzburg 1968; Wourms 1981; Grier et al. 2005). Spermatozeugmata are common in internally fertilizing teleosts (Grier et al. 1978; Downing and Burns 1995; Fishelson et al. 2007; Uribe et al. 2014).

Previous studies on black perch (*Embiotoca jacksoni*) have described multiple paternities of offspring by a given female, sperm competition, and population genetics (Reisser et al. 2009; Liu and Avise 2011; LaBrecque et al. 2014; Longo and Bernardi 2015; Johnson et al. 2016), but the basic reproductive biology of the black perch remains poorly understood. The black perch intromittent organs were first described by Agassiz (1853) who documented a smooth patch located on the anal fin with a surrounding sheath with a burrow to house the intromittent organ. The specific aims of our research note were to increase our understanding of the black perch reproductive biology. We have documented the progression of spermatocyte development and formation of the spermatozeugmata within the testicular tissue. Additionally, we have used histology to detail the association of the intromittent organs with the anal fin.

We used paraffin histological techniques to describe the black perch spermatocyte and intromittent organ morphology. Male black perch (111 ± 30 mm SL; 70–157 mm; $n = 8$) were collected from June to November 2014 in eel grass beds in Los Angeles, Orange, and San Diego Counties with at least two sites per location using a beach seine and hook and line methods. Fish were euthanized using an overdose of tricane methanesulfonate (MS-222) of a purity of at least 98% (1 g: 5,000 ml seawater). The testes and anal fin were dissected and preserved in Bouin's fixative and 10% neutral-buffered formalin, respectively, then transferred to 70% ethanol. Tissues were processed for paraffin histology by dehydration in a series of graded ethanols, cleared with xylene, and infiltrated and embedded with paraffin wax. Tissues were sectioned using a rotary microtome to a thickness of 5μm and stained with hematoxylin and eosin or Mallory trichrome stains. Tissues were examined using brightfield microscopy (Olympus BX60). Photos were taken using a digital camera (QICAM QImaging Fast 1394) and imaging software (Q-Capture Pro 7, QImaging, 2010). Fish were handled according to an approved protocol that followed the policies and guidelines of the California State University, Fullerton's Institutional Animal Care and Use Committee.

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Spermatocytes were staged according to previously published literature on embiotocids and other fishes (Gardiner 1978; Grier 1981; Schulz et al. 2010; Grier et al. 2005; Uribe et al. 2014). Black perch have an unrestricted lobular testis type (Uribe et al. 2005). Lobules are formed by sperm cells synchronously developing (i.e., at the same stage of spermatogenesis; Fig. 1). Interstitial tissue was observed between the lobules (Fig. 1). Primary spermatocytes had an enlarged nucleus and were held tightly together in a cyst (Fig. 1A), whereas the nuclei of secondary spermatocytes stained lighter than primary spermatocytes and their arrangement was not as rigid (Fig. 1B). Spermatids were characterized by a change in cell shape associated with the elongation of the nuclei and were smaller than spermatocytes (Fig. 1C). Spermatozoa are arranged into packets within the lumen of the lobule with sperm heads located at the perimeter and the tails (i.e., sperm flagella) pointed towards the center of the lumen (Fig. 1D). A dense aggregation of spermatozoa packets within the efferent ducts form a spermatozeugmata (Fig. 1E).

Examination of testicular micrographs of black perch ≥ 90 mm SL had testes that contained all stages of sperm development and spermatozeugmata within the lobules (Fig. 2A), indicating that they sexually mature and in a spawning capable/spawning reproductive phase (Brown-Peterson et al., 2011). Black perch < 90 mm SL did not have spermatozeugmata within the testicular tissues but all stages of spermatocyte development were present (Fig. 2B). These males were in a developing reproductive phase (Brown-Peterson et al., 2011).

The spermatozeugmata are presumable transferred into the female reproductive tract during copulation via one of the intromittent organs. Black perch intromittent organs are located on both sides of the anterior portion of the anal fin. Black perch < 90 mm SL did not have externally visible intromittent organs, however a smooth patch was observed on the anal fin (Fig. 3A). Wourms (1981) also notes that the intromittent organ is not present during the non-breeding season (i.e., winter), which we have also observed. In this case, the anal fin has no modification and looks like the fin of a black perch < 90 mm SL (pers. obs.). Black perch ≥ 90 mm SL had intromittent organs housed within a sheath located on both sides of the anterior portion of the anal fin (Fig. 3B). The intromittent organs of the fluffy sculpin (*Oligocottus snyderi;* Family Cottidae), a viviparous marine species, have been described as having a modified anal fin ray with the ability to bend in order to enter the female reproductive tract (Morris 1955). This is similar to the gonopodium of freshwater poeciliids, which also have a modified anal fin ray with specialized muscles that allow the gonopodium to rotate during copulation (Rosen and Gordon 1953). The anal fin of the male black perch does not appear to be modified and fin rays do not appear to be involved in sperm transfer. The intromittent organs form on a smooth area of the anal fin, parallel to the body (Fig. 3A). A fleshy sheath develops that houses the intromittent organ, which make up the bulbous protrusions on both sides of the anal fin that can be observed externally during breeding season (Fig. 3B).

Examination of the tissue of the anal fin of black perch < 90 mm SL that had not yet developed intromittent organs revealed that tissue of the presumptive intromittent organ was present (Fig. 4). Surrounding the intromittent organ tissue was loose and dense connective tissues (Fig. 4). Fin rays were observed but are not modified. It should be noted that although it appears that the anal fin rays are interrupted, the intromittent organ develops on the surface of the fin, thus fin rays can be observed in the surrounding tissue but are continuous. Histological examination of

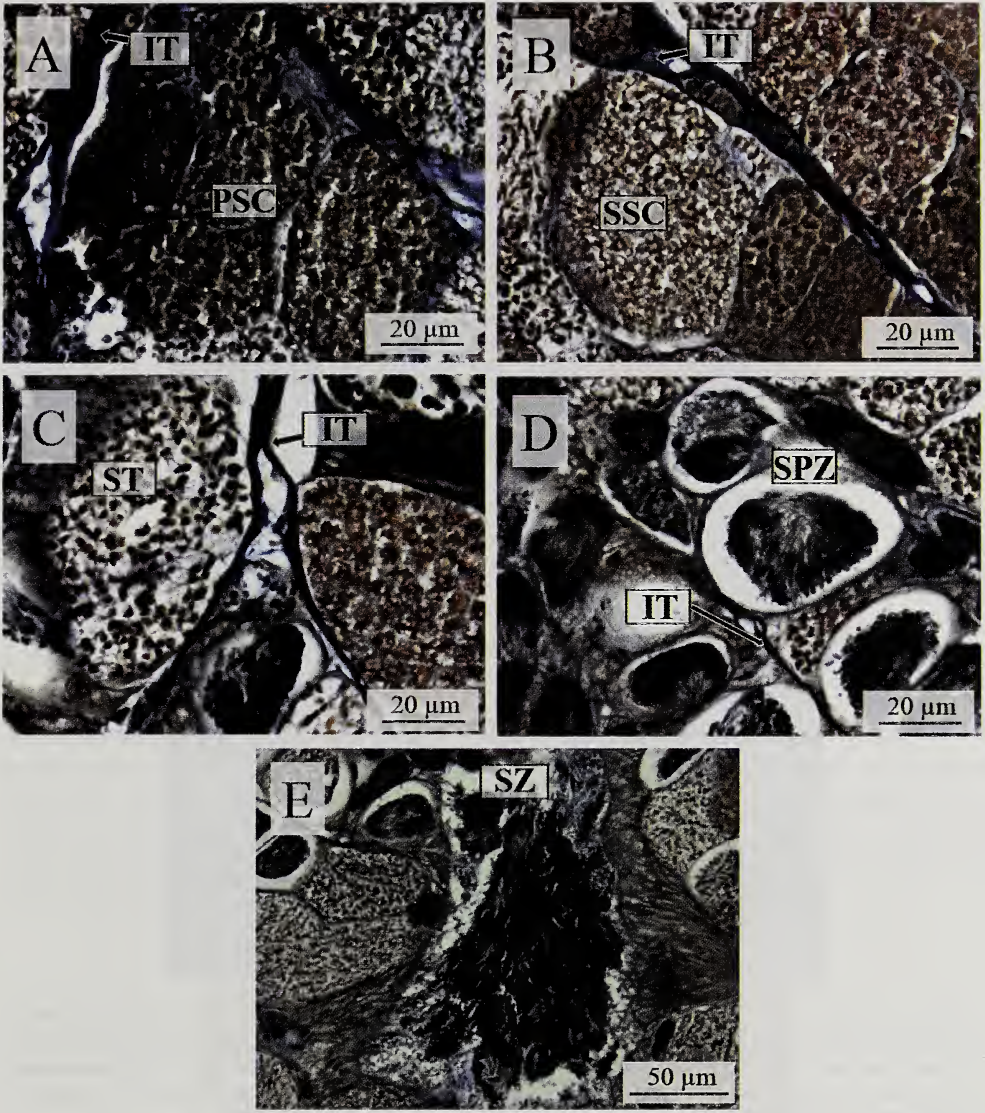

Fig. 1. Sperm cell developmental stages of black perch (*Embiotoca jacksoni*). A) Primary spermatocytes (40X); B) Secondary spermatocytes (40X); C) Spermatids (40X); D) Spermatozoa (40X); E) Spermatozeugmata (20X). All micrographs stained with Mallory trichrome. PSC = primary spermatocyte; SSC = secondary spermatocyte; ST = spermatid; SPZ = spermatozoa; SZ = spermatozeugmata; IT = interstitial tissue.

the intromittent organs of black perch ≥ 90 mm SL indicate they are surrounded by a protective sheath composed of smooth muscle (Fig. 5A). The outer layer of the sheath is composed of circular smooth muscle (Fig. 5A, B) with a layer of longitudinal smooth muscle (Fig. 5A, C). The smooth muscle layer is surrounded by an epithelial tissue (Fig. 5B). Dense fibrous connective tissue lies between the longitudinal smooth muscle and the intromittent organ (Fig. 5A, D). The intromittent organs are located on either side of a pair of fin rays (Fig. 5A, E). We hypothesize that the dense fibrous connective tissue surrounding the intromittent organs provides the structural

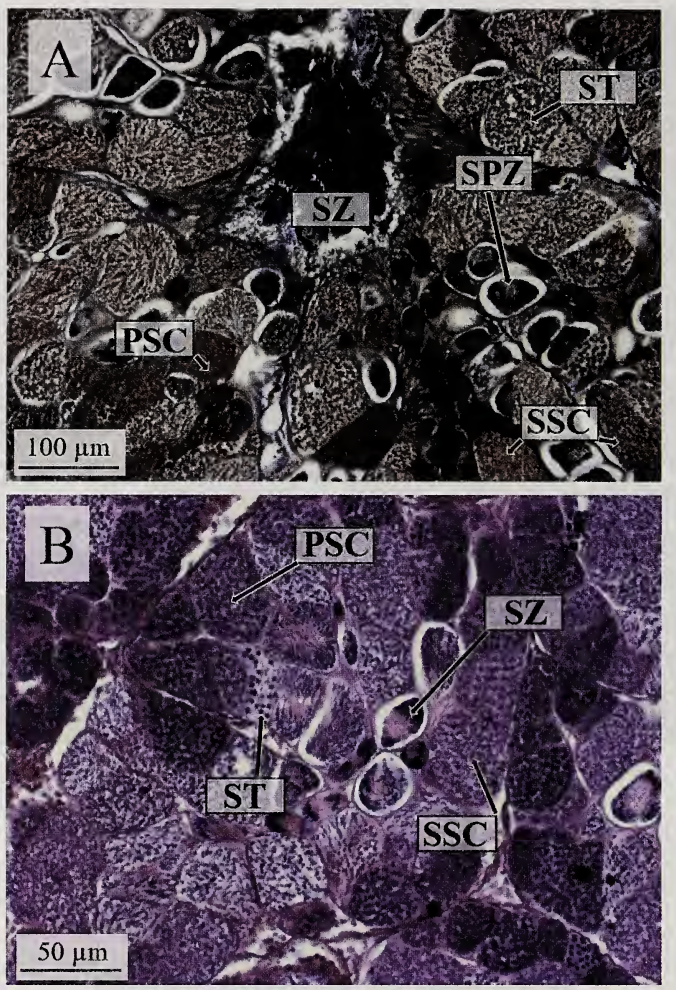

Fig. 2. Testicular micrographs of male black perch (*Embiotoca jacksoni*). A) Testes from males $\geq$ 90 mm SL contained all stages of spermatocyte development, including spermatozeugmata (10X; Mallory trichrome stain); B) Testes from smaller $<$ 90 mm SL contained all stages of spermatocyte development, but no spermatozeugmata (20X; hematoxylin and eosin). PSC = primary spermatocyte; SSC = secondary spermatocyte; ST = spermatid; SPZ = spermatozoa; SZ = spermatozeugmata.

support for the intromittent organ itself. Thus, smooth muscle contraction would act upon the intromittent organ forcing it out of the sheath.

The morphology of black perch intromittent organs is similar to the striped (*Embiotoca lateralis*) and pile perches (*Damalichthys vacca*; Blake 1868; pers. obs.) of the subfamily Embiotocinae. The shiner perch (subfamily Embiotocinae) have intromittent organs within a sheath similar to the black, striped, and pile perches and in addition have a single genital papilla (Fig. 6A; Wiebe 1968; Shaw 1971; Gardiner 1978). The barred (*Amphistichus argenteus)* and walleye *(Hyperprosopon argenteum*) surfperches (subfamily Amphistichinae) have been described as having only a genital papilla located on the ventral side of the body, anterior to the anal fin (Fig. 6B; Blake 1868; Carlisle et al. 1960; LaBrecque et al. 2014).

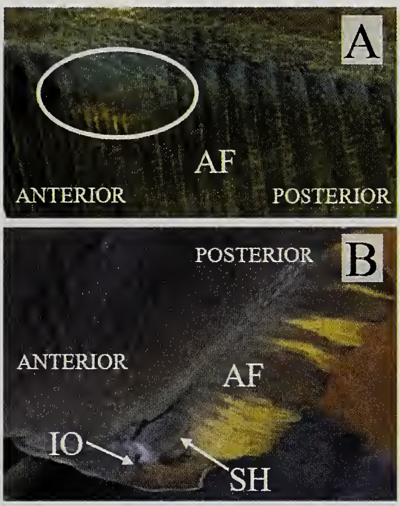

Fig. 3. Left, lateral view of the anal fin of male black perch (*Embiotoca jacksoni*). A) Anal fin of black perch < 90 mm SL; white circle represents location of developing intromittent organ and surrounding sheath; B) Anal fin of black perch ≥ 90 mm SL indicating the surrounding sheath that houses the intromittent organ. AF = anal fin; IO = intromittent organ; SH = sheath.

Our research note is the first to document the formation of black perch spermatozeugmata within the testis. Additionally, we have characterized the tissues of the intromittent organs and its muscular sheath which reside on an unmodified anal fin. We have identified several curious differences in male external reproductive structures between black perch and other embiotocids. We are conducting a more comprehensive study of the intromittent organs of the embiotocid family. We are also describing the functional anatomy of the female, particularly acceptance of the copulatory structure into the reproductive tract.

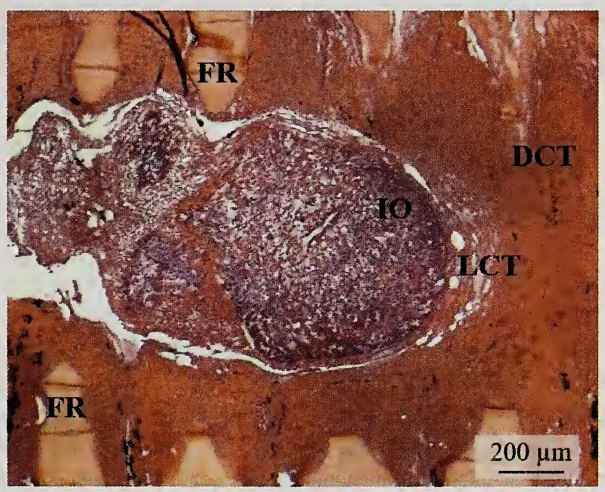

Fig. 4. Histological sagittal section of the anal fin of a black perch (*Embiotoca jacksoni*) < 90 mm SL stained with hematoxylin and eosin (4X). IO = intromittent organ; DCT = dense connective tissue; LCT = loose connective tissue; FR = fin ray.

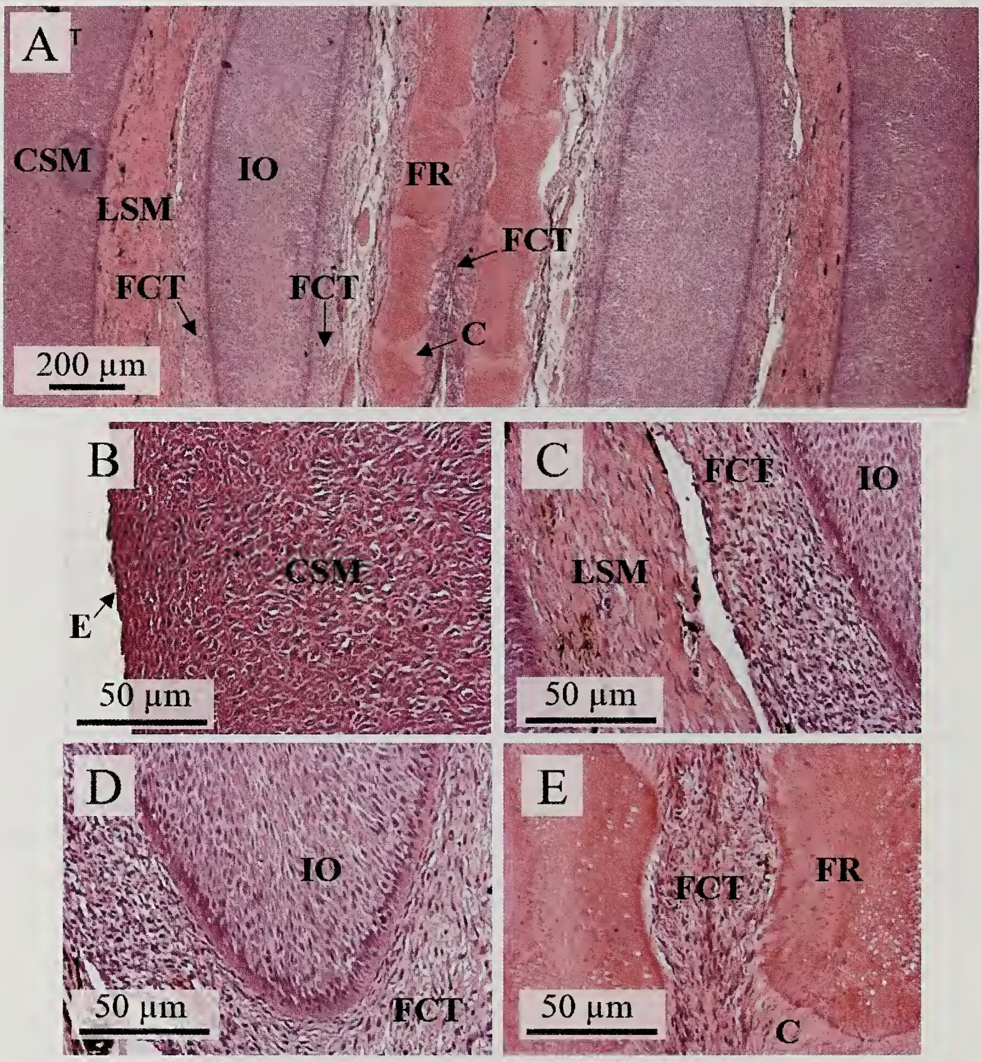

Fig. 5. Histological cross-section of the anal fin of a black perch (*Embiotoca jacksoni*) ≥ 90 mm SL stained with hematoxylin and eosin. A) Micrograph of the anal fin (4X); B) Circular smooth muscle (20X); C) Longitudinal smooth muscle and dense fibrous connective tissue (20X); D) Intromittent organ (20X); E) Fin rays and dense fibrous connective tissue (20X). CSM = circular smooth muscle; LSM = longitudinal smooth muscle; FCT = dense fibrous connective tissue; IO = intromittent organ; E = epithelium; FR = fin ray; C = cartilage.

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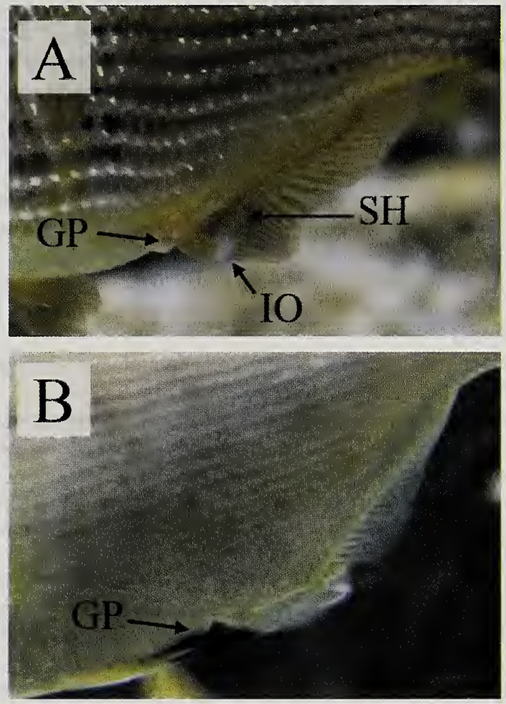

Fig. 6. Copulatory structures of two species of Embiotocids. A) Shiner perch (*Cymatogaster aggregata*) paired intromittent organs are housed within a surrounding sheath on the anterior portion of the anal fin and a single fleshy genital papilla located ventrally on the abdomen anterior to the anal fin (left side of body shown in figure); B) Walleye surfperch (*Hyperprosopon argenteum)* single genital papilla located ventrally on the abdomen anterior to the anal fin. IO = intromittent organ; SH = sheath; GP = genital papilla.

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